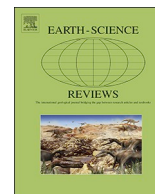




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Predation in the marine fossil record: Studies, data, recognition, environmental factors, and behavior

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ABSTRACT

The fossil record is the primary source of data used to study predator-prey interactions in deep time and to evaluate key questions regarding the evolutionary and ecological importance of predation. Here, we review the types of paleontological data used to infer predation in the marine fossil record, discuss strengths and limitations of paleontological lines of evidence used to recognize and evaluate predatory activity, assess the influence of environmental gradients on predation patterns, and review fossil evidence for predator behavior and prey defense. We assembled a predation database from the literature that documents a steady increase in the number of papers on predation since the 1960s. These studies have become increasingly quantitative and have expanded in focus from reporting cases of predation documented by fossils to using the fossil record of predation to test ecological and evolutionary hypotheses. The data on the fossil record of predation amassed so far in the literature primarily come from trace fossils, mostly drill holes and, to a lesser extent, repair scars, derived predominantly from the Cenozoic of Europe and North America. Mollusks are the clade most often studied as prey and inferred predators. We discuss how to distinguish biotic from abiotic damage and predatory from parasitic traces, and how to recognize failed predation. Our data show that identifying the predator is easiest when predator and prey are preserved in the act of predation or when predators were fossilized with their gut contents preserved. However, determining the culprits responsible for bite traces, drill holes, and other types of predation traces can be more problematic. Taphonomic and other factors can distort patterns of predation, but their potential effects can be minimized by careful study design. With the correct identification and quantification of fossilized traces of predation, ecological trends in predator-prey interactions may be discerned along environmental gradients in water depth, habitat, and oxygen and nutrient availability. However, so far, these trends have not been explored adequately for the fossil record. We also review the effects of climate change and ocean acidification on predator-prey interactions, but, again, few studies consider those factors from a deep-time perspective. Finally, fossils have been used successfully to infer the behavior of ancient predators and identify and interpret active and passive defense strategies employed by their prey. The marine fossil record of predation has become a major field of research over the last 50 years, but many critical gaps remain in our understanding of the evolutionary history of predator-prey interactions.

1. Introduction

Predation is viewed by many ecologists as one of the most important factors shaping marine ecosystems today (e.g., Langerhans, 2007; Paine, 1966). Similarly, many paleontologists consider predation to

have been a major force throughout the evolutionary history of marine ecosystems (e.g., Signor and Brett, 1984; Stanley, 2008; Vermeij, 1977), and ample evidence suggests that predator-prey interactions were common from the Neoproterozoic onward (e.g., Cohen and Riedman, 2018; Harper, 2006; Huntley and Kowalewski, 2007; Kelley et al., 2003;

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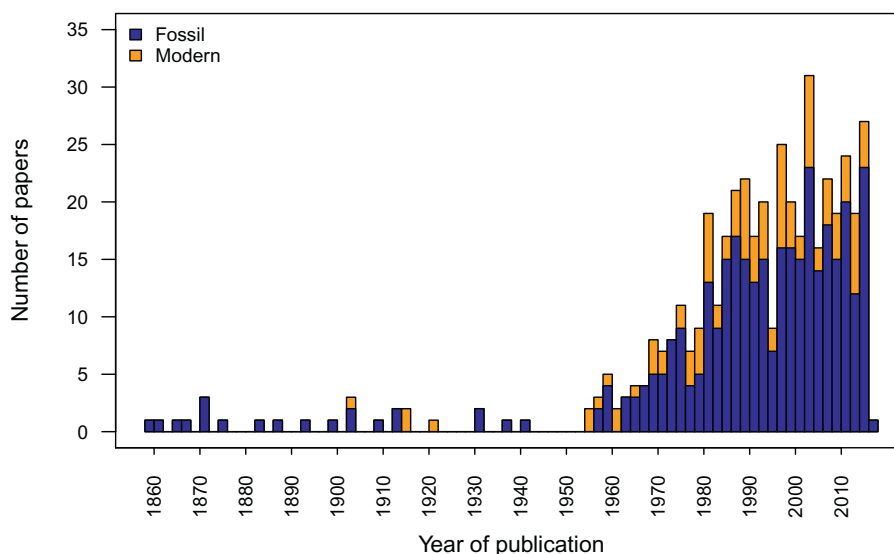


Fig. 1. The number of papers on evidence of predation in the marine fossil record in 2-year intervals based on our predation database ($n = 455$, of which 350 are fossil and 105 modern). “Modern” refers to studies based on live or recently dead specimens.

Klompmaker et al., 2017; Kowalewski et al., 1998; Kowalewski and Kelley, 2002; Signor and Brett, 1984; Vermeij, 1987). However, because predators are rarely preserved in the act of catching their prey, fossil evidence of predator-prey interactions is typically indirect (e.g., trace fossils). The correct recognition of predatory traces is paramount to infer the importance and evolution of predation in fossil ecosystems, but no comprehensive review exists regarding how to differentiate evidence of predation from damage caused by other processes (but see Kowalewski, 2002, for some aspects).

Once the evidence for predation has been recognized, patterns in predation can be investigated. Although predation is known to vary among environments today (e.g., Harper and Peck, 2016; Sanford, 1999; Sperling et al., 2013), relatively little attention has been paid to environmental gradients in predation in deep time, despite their potential influence on short- and long-term changes in predation intensity.

Recognizing evidence of predation is also crucial for interpreting the behavior of predators and their prey. Although interactions between predators and their prey can be observed directly today, deducing behavior is more difficult for fossil ecosystems. Nevertheless, trace fossils can be employed to infer predatory behavior in deep time, including the predator's selectivity of prey taxon, size, and site of attack (e.g., Bianucci et al., 2010; Kelley, 1988; Smith et al., 2018). Likewise, information about active and passive prey defenses may also be gleaned from the fossil record, with aid from observations in today's marine environment.

The goals of this paper are to (1) review the type of marine predation studies and data that are available from the fossil record, based on a predation database we assembled; (2) elucidate how to recognize evidence for predation and potentially confounding factors; (3) evaluate the influences of environmental gradients on predator-prey interactions today and in deep time; and (4) interpret the behavior of predators and their prey in ancient marine ecosystems. These aspects have either not been reviewed previously or were reviewed in the past but new research in the last decade warrants a reappraisal.

2. Predation database, history and types of studies, and types of data

2.1. Predation database

We assembled an occurrence-based database on the marine fossil record of predation, upon which the analyses in the next two sections of

this paper are based. We recorded the following data for each predation occurrence in the database: citation information for the predation study, type of evidence (e.g., drill holes), prey taxon, inferred predator, precise locality, stratigraphic level, and inferred age. The database also includes details not analyzed further herein, such as predation intensity, prey size, attack site on the victim, prey ecology, and lithology. The database was initially concentrated on evidence from predatory drill holes (predominantly ascribed to *Oichnus ovalis* Bromley, 1993, *O. paraboloides* Bromley, 1981, and *O. simplex* Bromley, 1981) and repair scars (partly attributable to *Caedichnus spiralis* Stafford et al., 2015), but recently was expanded to include data on other lines of paleontological evidence pertaining to predation that have become available. Some data from modern assemblages were included (though not as comprehensively) for comparison with the fossil data. Coprolites were rarely included in the database because of difficulty in determining their content and the taxonomic identity of the tracemaker. Parts of this database have been used previously (e.g., Huntley and Kowalewski, 2007; Klompmaker et al., 2017; Kowalewski et al., 1998).

2.2. History and types of studies

Studies on predation in the marine fossil record date back to at least 1858 (Buckland, 1858, cited in Massare, 1987). The number of published papers remained low until the 1960s. Since then, the pace of publications has increased steadily and continuously (Fig. 1). Early publications focused on documenting biotic interactions. Later papers used such records to test hypotheses or validate specific predictions of evolutionary paleoecology. The development of the concepts of coevolution and escalation in the 1970s and 1980s (e.g., Dawkins and Krebs, 1979; Smith, 1976; Vermeij, 1977, 1987) fostered tests based on the fossil record, which are probably reflected in the post-1960 rise in the published literature (Fig. 1). More recently, studies of predation in deep time have evaluated macroevolutionary effects of predation (e.g., Dietl and Kelley, 2002; Huntley and Kowalewski, 2007; Jablonski, 2008; Nagel-Myers et al., 2013; Roy, 1996), documented predation on taxa that had not been identified as viable prey or were previously largely overlooked in the fossil record (e.g., Baumiller, 1990, 1996; Baumiller and Bitner, 2004; Bicknell et al., 2018; Gordillo, 2013a; Klompmaker, 2011, 2012; Klompmaker et al., 2013, 2014, 2015; Kowalewski et al., 2005; Rojas et al., 2014, 2017), and explored geologic times and geographic localities that are relatively less known for their predation record (e.g., Chattopadhyay and Dutta, 2013;

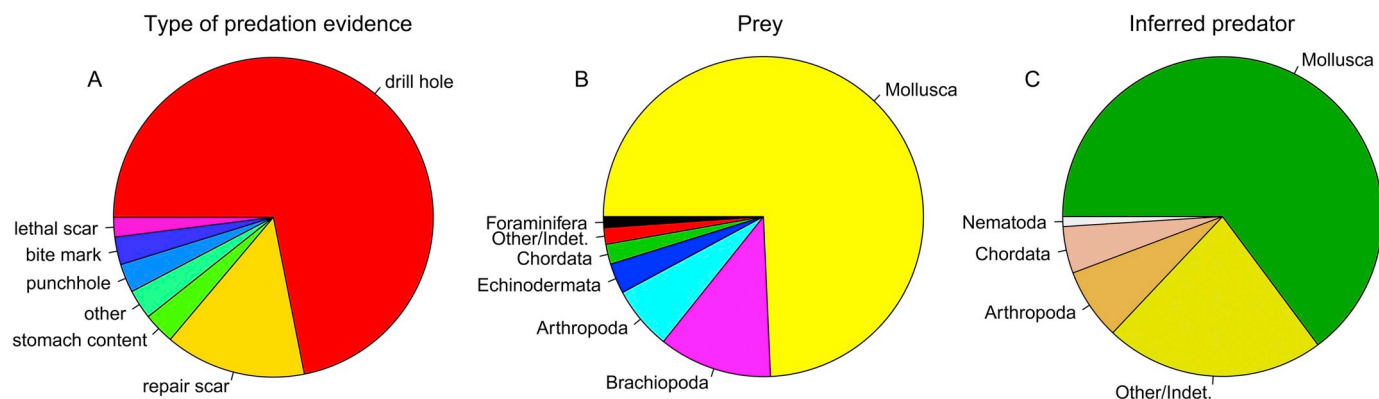


Fig. 2. Prey occurrences in the marine fossil record in our predation database split by (A) types of predation evidence, (B) prey, and (C) inferred predators. $n = 3380$.

Kowalewski et al., 1998, 2000; Mallick et al., 2017; Morris and Bengtson, 1994; Villegas-Martín et al., 2016). Many of these studies established temporal trends in predation by compiling data from the existing literature or by processing bulk samples to develop large-scale datasets on predation traces (e.g., Huntley and Kowalewski, 2007; Kelley and Hansen, 2003; Klompmaker et al., 2017). More research should focus on geologic times (pre-Cretaceous) and geographic regions that remain poorly studied, such as Africa, parts of Asia, South America, and Antarctica. Additionally, there is a strong focus on reporting positive evidence of predation, while research on negative evidence or low predation intensities (e.g., Forel et al., 2018; Klompmaker et al., 2016a; Tackett and Tintori, 2019) is equally important to assess temporal trends of predation intensity.

Neontological studies often involved experiments in which predator-prey interactions were monitored to develop and/or evaluate hypotheses of evolutionary or paleontological significance. A major share of such studies has been performed on molluscan predator-prey systems (e.g., Ansell, 1982a, 1982b, 1982c; Das et al., 2015; Edwards and Huebner, 1977; Hart and Palmer, 1987; Hughes and Dunkin, 1984; Peharda and Morton, 2006); experimental work was also common on durophagous predation by crustacean predators on molluscan or arthropod prey (Barbeau and Scheibling, 1994; Ebling et al., 1964). Fewer studies have examined echinoderms and cnidarians as predators or as prey (e.g., Paine, 1976; Riedel et al., 2008a). Similar lines of ecological investigation have also been pursued in nature rather than in a lab setting (e.g., Aronson, 1989; Dietl and Alexander, 1995, 1997; Kingsley-Smith et al., 2003; Palmer, 1979; Riedel et al., 2008a; Sawyer et al., 2009; Schindler et al., 1994; Vignali and Galleni, 1986).

These studies on modern organisms are crucial in understanding ancient predator-prey interactions. Such studies often discover specific behavioral patterns of extant predators, including selectivity of prey taxon, size, and attack site on the prey – many of which have also been established subsequently in the fossil record of predation. Prey response, including morphological and behavioral defenses, has also been documented in experimental settings (Rovero et al., 1999; Smith and Jennings, 2000). Because the time required for the prey to develop morphological responses is often years longer than the typical duration of experiments, the number of studies exploring morphological changes of prey is small compared to behavioral studies. Only a few studies have combined neontological and paleoecological observations to evaluate specific aspects of biotic interactions, such as research on naticid gastropod predators (Chattopadhyay et al., 2014a; Kitchell et al., 1981). Other neontological studies have used organismal remains to understand the taphonomic aspects of the fossil record of predation and establish guidelines for identifying taphonomically altered assemblages (see Section 3.5).

2.3. Types of data

The main strategies that marine predators use to catch prey are whole organism ingestion, insertion (e.g., of an appendage into the prey) and extraction, pre-ingestive breakage, and drilling (e.g., Harper and Skelton, 1993a; Vermeij, 1987). The first two methods, however important and common in modern marine ecosystems, are rarely recognizable in the fossil record. Hence, the study of fossil predation understandably focuses on the last two types of predation events, which leave recognizable traces. Consequently, the occurrence-based record is dominated by trace fossils such as drill holes (75.8%) and repair scars (12.3%), whereas direct evidence represented by predator digestive tract contents (e.g., bromalites and contents preserved in place) is much rarer (2.6%; Fig. 2A).

Most marine prey items recorded in the literature represent invertebrates, although vertebrate prey are known, primarily from preserved stomach contents or scavenging- and/or predation-related bite marks (or bite traces sensu Vallon et al., 2015) on bones of fish (e.g., Amalfitano et al., 2017; Claeson et al., 2015; Collareta et al., 2017a; Hunt and Lucas, 2014; McHenry et al., 2005), reptiles (e.g., Milàn et al., 2011; Noriega et al., 2007; Noto et al., 2012; Rothschild et al., 2018), and mammals (e.g., Boessenecker and Perry, 2011; Deméré and Cerutti, 1982; Ehret et al., 2009). Some of the first documented examples of predation in the fossil record involve vertebrate prey (e.g., Buckland, 1858; Capellini, 1865; Cope, 1868, 1871, 1872; Dollo, 1887; Portis, 1883). Overwhelmingly, however, prey occurrences (Fig. 2B) are dominated by mollusks (77%), followed by brachiopods (9.9%) and arthropods, mostly ostracods (6.2%). Inferred predator occurrences (Fig. 2C) consist primarily of mollusks (69.2%, predominantly drilling gastropods), but arthropods (6.1%, primarily decapod crustaceans) and chordates (3.9%, mostly marine reptiles) are also commonly reported. In 20% of the cases, the predator was either unidentified or, on rare occasions, was ascribed to another taxonomic group (e.g., Cambrian priapulids). In short, the fossil record of marine predation, as reported, is dominated by gastropods that drill their mollusk prey, followed by decapod crustaceans that break mollusk shells. More work is needed on types of predation other than drilling and shell crushing.

Most reports of predation in the fossil record come from western Europe, the United States, and Japan (Fig. 3). This pattern is roughly comparable to occurrences of marine metazoans in the Paleobiology Database (e.g., Alroy et al., 2001). Stratigraphically, very few prey occurrences are known from the Neoproterozoic (Fig. 4, all prey), except for holes in Ediacaran *Cloudina* (Bengtson and Zhao, 1992; Brain, 2001; Hua et al., 2003) and in Tonian microorganisms (Porter, 2016). More occurrences are known from the Paleozoic and early Mesozoic; a further increase starting in the mid-Cretaceous continues into the Cenozoic, consistent with a previous analysis using drill-hole data only (Kowalewski et al., 1998). The late Cenozoic (Neogene and Quaternary) contains as much as 49.0% of all fossil prey occurrences in our

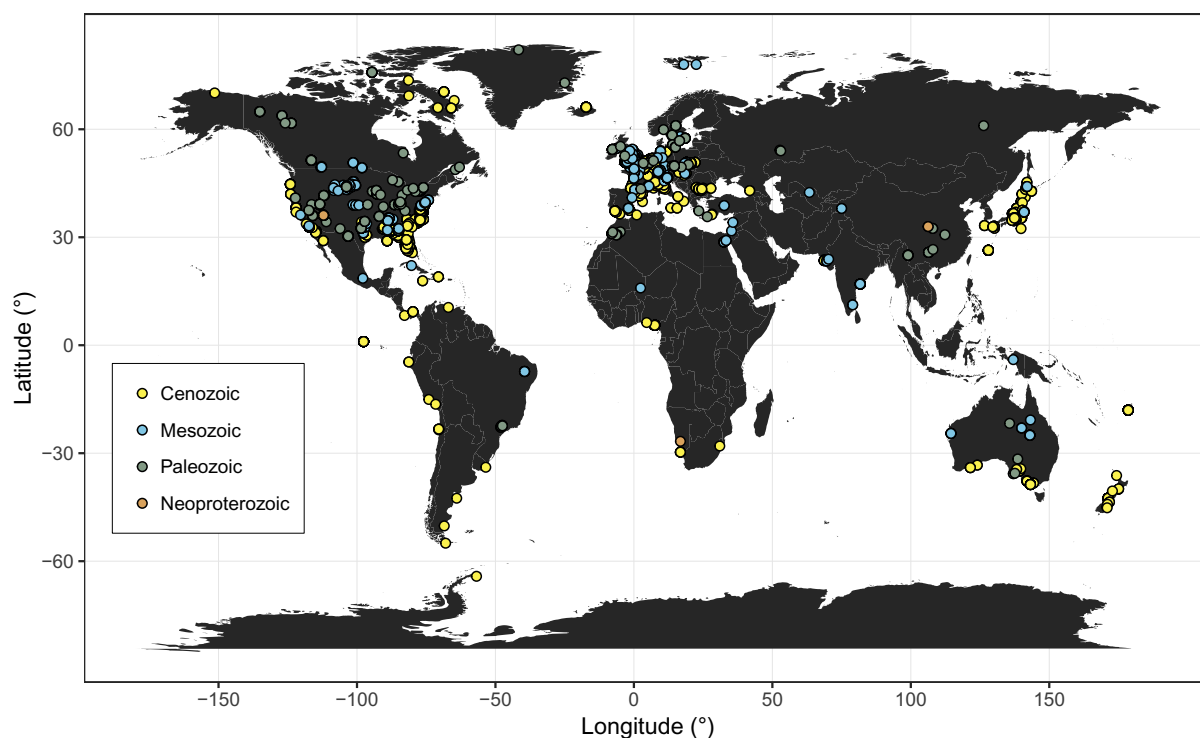


Fig. 3. Geographic location of occurrences of predation on metazoans from the marine fossil record (Neoproterozoic – non-Recent Holocene) per era from our predation database. Older occurrences are plotted on top of younger ones (covering many Cenozoic occurrences). n total = 3380: Cenozoic = 2237, Mesozoic = 677, Paleozoic = 443, Neoproterozoic = 23.

database, most of which are shallow marine. Although research has concentrated on predator-prey interactions in the Cretaceous–Cenozoic, this temporally unbalanced focus at least partly reflects the dramatic post-Paleozoic increase in the presence of drilling predators and durophagous decapod crustaceans (e.g., Schweitzer and Feldmann, 2010; Walker and Brett, 2002).

The peak in prey occurrences in the late Cenozoic is caused nearly entirely by Mollusca and to some extent by Arthropoda (Fig. 4). Conversely, brachiopod prey occurrences are most abundant in the Paleozoic (Fig. 4), mirroring their relatively high diversity and abundance in that era (e.g., Blois et al., 2013; Payne et al., 2014). Thus, of the shelly benthic prey, it appears that brachiopods were more common prey than mollusks in the Paleozoic, but the opposite applies for the Cenozoic. This pattern is partly reflected in relative drilling intensities within Paleozoic and Cenozoic assemblages that contain both groups (Hoffmeister et al., 2004; Leighton et al., 2013; Simões et al., 2007). Prey occurrences for Echinodermata and Chordata are fewer and increase slightly toward the present (Fig. 4).

Within the diverse phyla, various prey clades have been recognized (see Table 1 for an overview of the literature, particularly for clades that are common prey). In addition to bivalve and gastropod mollusks, which are represented abundantly in the literature, many other clades served as prey. Rare prey occurrences in the marine fossil record are represented by taxa such as Polyplacophora, Xiphosurida, Hoplocarida, Phyllocarida, Eurypterida, Homalozoa, Osteostraci, Agnatha, Aves, Bryozoa, Cnidaria, Graptolithina, and Porifera, and even for taxa that did not inhabit the marine environment (Pterosauria, Dinosauria). Thus far, we have not been able to find references to predation in the fossil record of Rostroconchia, Holothuroidea, Pycnogonida, Edrioasteroidea, and Cystoidea. Many of these clades with rare or no marine predation record do not have an extensive fossil record due to low preservation potential (e.g., Holothuroidea), short stratigraphic range (Cystoidea, Osteostraci), low diversity (Xiphosurida), and/or rarity in marine settings (Pterosauria, Dinosauria). In other cases, more diverse and abundant phyla such as Porifera and Cnidaria may suffer from a lack of

research targeting predation. Indeed, studies published in the last 10–15 years have shown that predation may be much more common than previously thought for multiple, previously underappreciated prey groups. These include Cirripedia (e.g., Gordillo, 2013a; Klompmaker et al., 2015), Scaphopoda (Klompmaker, 2011; Li et al., 2011; Mallick et al., 2017), Annelida (Klompmaker, 2012; Martinell et al., 2012; Villegas-Martín et al., 2016), Decapoda (Klompmaker et al., 2013; Pasini and Garassino, 2012), Tentaculita (Vinn, 2009, 2012), and Conodonts (Choo et al., 2009; Zatoń et al., 2017; Zatoń and Rakociński, 2014).

3. Recognizing and identifying predation

3.1. Biotic and abiotic shell damage

Bromalites of carnivores (fossilized products of digestion, including cololites, coprolites, enterospirae, gastrolites, and regurgitalites; see Hunt, 1992) provide relatively unequivocal evidence of biotic activities when properly recognized. Drawing a distinction between biotic and abiotic traces can be more challenging for shell and bone damage, such as circular to irregular holes, shell fragments, non-lethal scars, and bite marks. Nevertheless, a number of general criteria can be used to establish a biotic origin of such traces (expanded from Kowalewski, 2002). These include: (1) distinct geometric shape; (2) narrow size range; (3) geometry consistent with penetrative activities aimed at gaining access to tissue inside protective housing; (4) non-random distribution across prey taxa; (5) non-random spatial distribution on prey skeletons (behavioral stereotypy); (6) non-random distribution across prey size classes; (7) presence of complementary scars on both sides of the prey; (8) presence of attachment scars; (9) correlation between trace size and prey size; (10) presence of the hypothesized trace maker in the same stratigraphic unit as the trace; (11) morphological similarity to traces made by extant predators or parasites; and (12) absence of unequivocal evidence for abiotic damage. More detailed criteria for each trace type are discussed below.

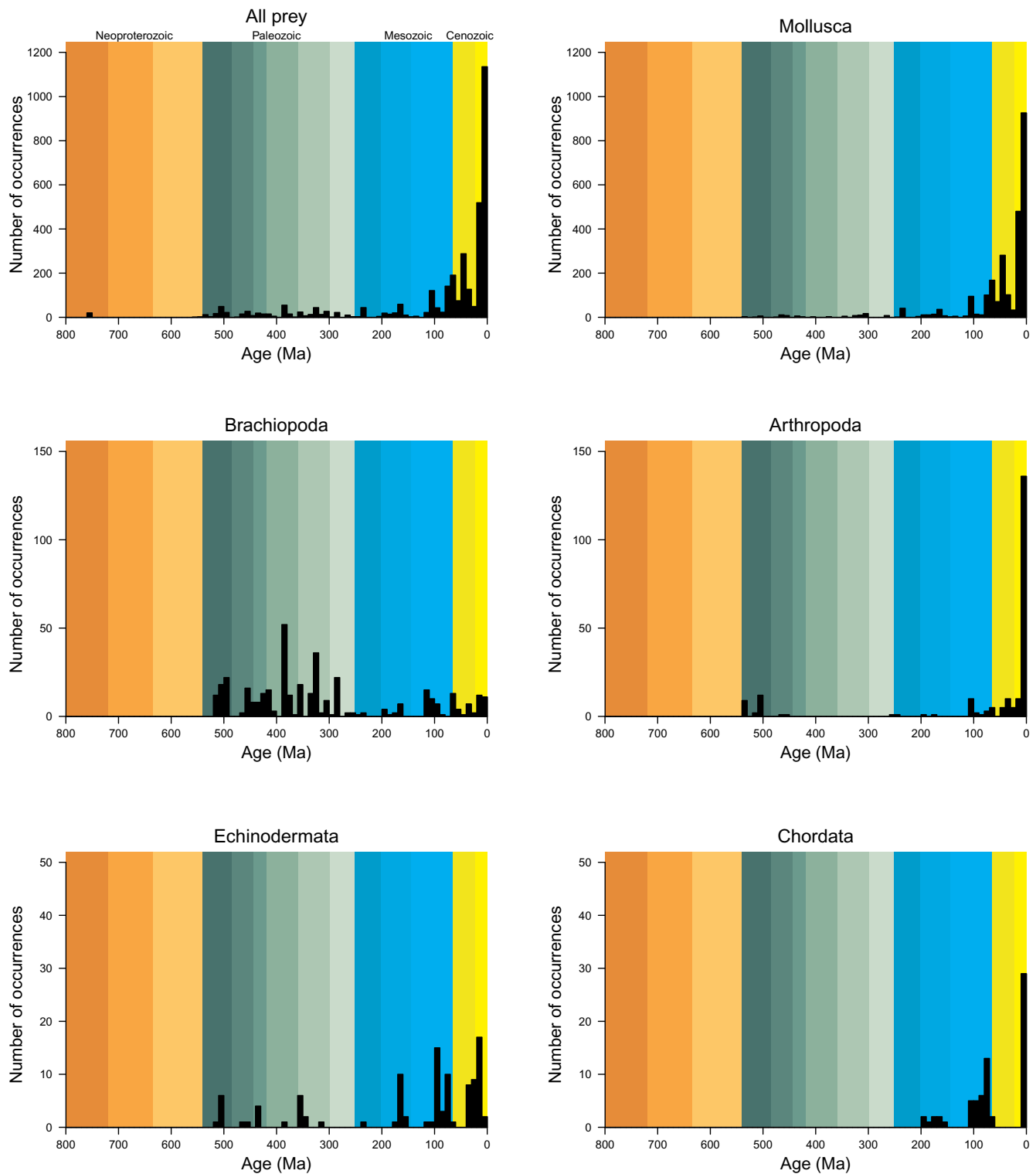


Fig. 4. The number of occurrences of predation in the marine fossil record throughout the Geozoic in 10-my intervals for all prey ($n = 3380$) and common prey phyla. Each period is highlighted by a different color shade within eras.

3.1.1. Circular and irregular holes

Millimeter to centimeter-sized (sub)circular holes in shells are created by predators such as drilling organisms (Klompmaker et al., 2017; Kowalewski, 2002), stomatopods (Geary et al., 1991; Pether, 1995), crabs (Fraaye, 1996; Krantz and Chamberlin, 1978; Turra et al., 2005), humans (Kubicki et al., 2017), birds (Cadée, 1994; Harper and Kelley, 2012), fishes (Norton, 1988; Rasser and Covich, 2014), durophagous

cephalopods (Klompmaker et al., 2009; Takeda et al., 2016), sharks (Mapes et al., 1989, 1995), and mosasaurs (Kauffman and Kesling, 1960; Tsujita and Westermann, 2001). Boring, including by domicile-seekers, may result in non-predatory holes (Ebbestad and Tapanila, 2005; Richards and Shabica, 1969; Wilson and Palmer, 2001). Holes or perforations are also created by abiotic processes, including pressure solution due to compaction of sediments (Lescinsky and Benninger,

Table 1

A non-comprehensive overview of prey in the marine fossil record, arranged alphabetically. For common prey (e.g., bivalves, gastropods), only references with extensive quantitative data are listed.

| Prey phylum | Lower-ranked prey clade | References |
|---------------|-------------------------|--|
| Annelida | | e.g., Conway Morris, 1990; Klompmaker, 2012; Martinell et al., 2012; Müller, 1969; Vannier, 2012; Villegas-Martín et al., 2016; Zatoń and Rakociński, 2014 |
| Arthropoda | Cirripedia | e.g., Donovan and Novak, 2015; Gale and Sørensen, 2015; Gordillo, 2013a; Klompmaker et al., 2014, 2015; Kočí et al., 2015 |
| Arthropoda | Decapoda | e.g., Bishop, 1972, 1975; Ishikawa et al., 2004; Jäger and Fraaye, 1997; Klompmaker et al., 2013; Maisey, 1994; Pasini and Garassino, 2012 |
| Arthropoda | Eurypterida | Caster and Kjellesvig-Waering, 1964 |
| Arthropoda | Hoplocarida | Lund and Lund, 1984, 1985 |
| Arthropoda | Ostracoda | e.g., Aranki, 1987; Bhatia et al., 1989; Maddocks, 1988; Reyment et al., 1987; Reyment and Elewa, 2003; Ruiz et al., 2010a, 2010b; Villegas-Martín et al., 2019 |
| Arthropoda | Phyllocarida | Briggs et al., 2011; Broda et al., 2018 |
| Arthropoda | Thylacocephala | Briggs and Rolfe, 1983; Broda et al., 2015; Pinna et al., 1985; Williams, 1990; Zangerl and Richardson, 1963 |
| Arthropoda | Trilobita | e.g., Alpert and Moore, 1975; Babcock, 1993, 2003; Briggs et al., 1994; Conway Morris and Jenkins, 1985; Kimmig and Pratt, 2018; Ludvigsen, 1977; Nedin, 1999; Pates et al., 2017; Pates and Bicknell, 2019; Pratt, 1998; Zhu et al., 2004 |
| Arthropoda | Xiphosurida | Bicknell et al., 2018 |
| Brachiopoda | | e.g., Alexander, 1986a; Daley, 2008; Forcino et al., 2017; Harper and Wharton, 2000; Kowalewski et al., 2000; Leighton, 2003a, 2003b; Rojas et al., 2017; Smith et al., 1985; Tuura et al., 2008 |
| Bryozoa | | Berning, 2008; McKinney et al., 2003; Taylor, 1982; Wilson and Taylor, 2006 |
| Chordata | Acanthodii | Arsenault, 1982; Davidson and Trewin, 2005; Janvier, 1996, pp. 297–300; Miles and Westoll, 1968, p. 462 |
| Chordata | Agnatha | Lebedev et al., 2009 |
| Chordata | Aves | Martin and Bjork, 1987 |
| Chordata | Chondrichthyes | e.g., Bjork, 1981; Hlavin, 1990; Wahl, 2005; Williams, 1990 |
| Chordata | Conodonts | Choo et al., 2009; Conway Morris, 1990; Nicoll, 1977; Williams, 1990; Zatoń et al., 2017; Zatoń and Rakociński, 2014 |
| Chordata | Dinosauria | Taylor et al., 1993: predation or scavenging |
| Chordata | Mammalia | e.g., Bianucci et al., 2010; Boessenecker and Perry, 2011; Ehret et al., 2009; Kallal et al., 2012; Portis, 1883; Voss et al., 2019 |
| Chordata | Osteichthyes | e.g., Bardack, 1965; Buckland, 1858; Cicimurri and Everhart, 2001; Collareta et al., 2015, 2017b; Cope, 1868; Ebert et al., 2015; Kear et al., 2003; Maisey, 1994; McAllister, 2003; McHenry et al., 2005; Viohl, 1990; Wretman and Kear, 2014 |
| Chordata | Osteostraci | Denison, 1956, pp. 425–426 |
| Chordata | Placodermi | e.g., Dennis and Miles, 1981; Lebedev et al., 2009; Long, 1995, pp. 189–190; Zakharenko, 2008 |
| Chordata | Pterosauria | Brown, 1904 |
| Chordata | Reptilia | e.g., Amalfitano et al., 2017; Cope, 1872; Eastman, 1964; Everhart, 2008; Kear et al., 2003; Konishi et al., 2011; Massare, 1987; Myrvold et al., 2018; O'Keefe et al., 2009; Rothschild et al., 2018; Tschanz, 1989 |
| Cnidaria | | e.g., Babcock et al., 1987; Galle and Ficner, 2004; Galle and Mikuláš, 2003; Mapes et al., 1989; Webb and Yancey, 2010; Wood, 2003 |
| Echinodermata | Asteroidea | e.g., Breton, 1992; Lehmann, 1951; Neumann, 2000; Wright and Wright, 1940; Zatoń et al., 2007 |
| Echinodermata | Blastoidea | Parasitic drill holes most likely: Baumiller, 1993, 1996; Macurda, 1965; Meyer and Macurda, 1977 |
| Echinodermata | Crinoidea | e.g., Baumiller et al., 2010a; Baumiller and Gahn, 2003, 2004; Brachanec et al., 2017; Gahn and Baumiller, 2005; Lehmann, 1975; Syverson et al., 2018; Thomka and Eddy, 2018; Zatoń et al., 2007 |
| Echinodermata | Echinoidea | e.g., Beu et al., 1972; Ceranka and Zlotnik, 2003; Gibson and Watson, 1989; Gripp, 1929; Grun et al., 2017; Kowalewski and Nebelsick, 2003; McNamara, 1994; Wilson et al., 2015; Zinsmeister, 1980; Zlotnik and Ceranka, 2005 |
| Echinodermata | Homalozoa | Deline, 2008: parasitic or predatory |
| Echinodermata | Ophiuroidea | e.g., Aronson, 1987, 1991, 1992; Aronson et al., 1997; Hess, 1960; Lehmann, 1951; Zatoń et al., 2008 |

(continued on next page)

Table 1 (continued)

| Prey phylum | Lower-ranked prey clade | References |
|------------------|--------------------------|---|
| Foraminifera | | e.g., Collen, 1973; Culver and Lipps, 2003; Hageman and Kaesler, 2002; Herrero and Canales, 2002; Lehman, 1971; Malumián et al., 2007; Nielsen and Nielsen, 2001; Sliter, 1971; Syed et al., 2014 |
| Hemichordata | Graptolithina | Loydell et al., 1998; Muir and Botting, 2007; Underwood, 1993 |
| Mollusca | Bivalvia | e.g., Adegoke and Tevesz, 1974; Alexander and Dietl, 2003; Chattopadhyay et al., 2016; Chattopadhyay and Baumiller, 2010; Dietl, 2004; Fischer, 1966; Harper, 1994; Hoffman et al., 1974; Kelley et al., 2001; Kelley and Hansen, 1993, 2003; Klompmaker, 2009; Klompmaker et al., 2016a; Kojumdjieva, 1974; Kowalewski, 1990; Leonard-Pingel and Jackson, 2016; Ozanne and Harries, 2002; Taylor, 1970; Taylor et al., 1983 |
| Mollusca | Cephalopoda | e.g., Andrew et al., 2015; Bond and Saunders, 1989; Hansen and Mapes, 1990; Kauffman and Kesling, 1960; Klompmaker et al., 2009; Klug and Vallon, 2018; Kröger, 2002, 2004; Landman and Waage, 1986; Mapes et al., 1995; Mapes and Chaffin, 2003; Martill, 1990; Pollard, 1968; Sato and Tanabe, 1998; Takeda et al., 2016 |
| Mollusca | Gastropoda | e.g., Adegoke and Tevesz, 1974; Alexander and Dietl, 2003; Allmon et al., 1990; Bafuk and Radwański, 1996; Chattopadhyay et al., 2016; Chattopadhyay and Baumiller, 2010; Fischer, 1966; Hagadorn and Boyajian, 1997; Hoffman et al., 1974; Hoffman and Martinell, 1984; Kelley et al., 2001; Kelley and Hansen, 2003; Kohn and Arua, 1999; Kojumdjieva, 1974; Kowalewski, 1990; Mallick et al., 2014; Maxwell, 1988; Taylor, 1970; Taylor et al., 1983; Vermeij and Dudley, 1982; Walker, 2001 |
| Mollusca | Helcionelloida | Skovsted, 2004; Skovsted et al., 2007 |
| Mollusca | Hyalolitha | e.g., Baumiller et al., 2010b; Briggs et al., 1994; Conway Morris, 1979; Kimmig and Pratt, 2018; Malinky and Skovsted, 2004 |
| Mollusca | Polyplacophora | Rojas et al., 2014 |
| Mollusca | Scaphopoda | e.g., Klompmaker, 2011; Li et al., 2011; Mallick et al., 2017; Robba and Ostinelli, 1975; Yochelson et al., 1983 |
| Mollusca | Tergomya | Ebbestad et al., 2009 |
| Porifera | | Blake and Elliott, 2003; Elliott, 2008 |
| phylum uncertain | Cloudinidae | Becker-Kerber et al., 2017; Bengtson and Zhao, 1992; Brain, 2001; Hua et al., 2003 |
| | Mobergellidae | Bengtson, 1968 |
| | Tentaculita | Berkyová et al., 2007; Larsson, 1979; Vinn, 2009, 2012 |
| | Neoproterozoic Eukaryota | Porter, 2016 |

1994) and abrasion, as observed in natural and experimental settings (Brom, 2014; Cadée, 2016; Chojnacki and Leighton, 2014; Gorzelak et al., 2013; Salamon et al., 2014).

Distinguishing biotic from abiotic holes is simplest for circular drill holes. Holes produced by abrasion tend to be more irregular and less smooth than predatory or parasitic holes (Brom, 2014; Chojnacki and Leighton, 2014; Salamon et al., 2014) and also lack rasp marks produced by radular teeth (Schiffbauer et al., 2008) and beveled edges characteristic of drill holes produced by naticid gastropods (Kelley and Hansen, 2003). Drill holes produced by cassid gastropods in echinoid prey are exceptions; because prey tests consist of small calcitic plates, drill-hole boundaries tend to be irregular (Kowalewski and Nebelsick, 2003; Nebelsick and Kowalewski, 1999). Predatory and parasitic drill holes in otherwise complete gastropod shells can be widened by abrasion, and their distinct geometric signatures (e.g., smooth regular margins, beveled edges) may be obscured or obliterated, but only after prolonged tumbling (~144 h, Chojnacki and Leighton, 2014). Circular holes between the septa of ammonite phragmocones, chambers containing gas and water rather than soft tissue, were interpreted as evidence of implosion (Keupp, 1991).

Irregular holes of biotic origin can be more difficult to distinguish from holes induced abiotically, but there are ways to minimize confusion. Pressure solution is likely to have occurred when damage resembles the cross-sectional outline of plicate shells and specimens contain an embedded shell (Lescinsky and Benninger, 1994). Specimens with abrasion-induced holes can show evidence of thinning of the shell around the hole (Brom, 2014; Chojnacki and Leighton, 2014), which is rarely observed for irregular holes produced by predators (Geary et al., 1991; Pether, 1995; Turra et al., 2005). Additionally, absence of

abrasion or other signs of transport or reworking in otherwise pristine shells favors a biotic interpretation of the holes. For *Nautilus* shells, tumbling experiments resulted in irregular holes on the ventral side of the phragmocone and in the body chamber that appear relatively straight in lateral view (Wani, 2004). Inferred ventral bite marks in ammonites (Andrew et al., 2010; Klompmaker et al., 2009; Takeda et al., 2016) are found exclusively on the body chamber, and such damage reaches much deeper into the body whorl (i.e., is much more angular in lateral view). Similarly, vertebrate bite marks in shells and bones of their prey most often show distinct depressions that can be related explicitly to the dental and jaw morphology of the predator (e.g., Bianucci et al., 2010; Boessenecker and Perry, 2011; Kear and Godthelp, 2008).

3.1.2. Shell fragments

Shell fragments can be produced by both abiotic processes and shell-crushing predators, including arthropods, cephalopods, and a variety of vertebrates (Brett and Walker, 2002; Cadée, 1994; Walker and Brett, 2002; see also Zuschin et al., 2003, for a review of abiotic and biotic shell breakage). Abiotic factors that produce shell fragments include compaction, tectonic shear, impacts from shells and other objects, and implosion (Checa, 1993; Klompmaker, 2009; Leighton et al., 2016; Shanks and Wright, 1986; Wani, 2004; Zuschin et al., 2003); such fragments can be modified by impacts and abrasion, primarily in the surf zone or during storms. In lithified sediments, compaction and tectonic shear are generally easy to recognize because broken parts remain next to one another. Unlike for lithified sediments, breakage due to compaction in unlithified sediments (Fig. 5) can be more challenging to distinguish from other types of breakage, as pieces from a

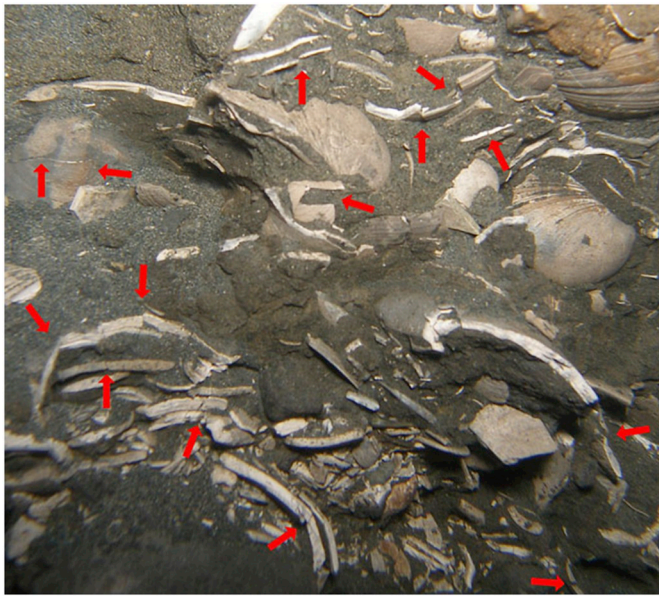


Fig. 5. Possible evidence of breakage due to compaction (see arrows) of Pliocene bivalves from the Mill-Langenboom locality in the Netherlands. Underwater photo is from a subvertical wall in an artificial lake. Photo by Ron Derks.

single shell disassociate during collecting and processing of samples. Compaction can result in angular fragments, as shown experimentally for scaphopods and bivalves (Klompaker, 2011; Kosloski, 2011; Zuschin and Stanton, 2001), or breakage along growth lines of *Nautilus* shells (Wani, 2004). Kosloski (2011) showed that, for the bivalve *Mercenaria mercenaria*, fragments caused by compaction can be differentiated from those caused by a predator. Specifically, fragments formed under uniaxial compression display plumose structures in homogeneous inner shell layers and step-like breakage patterns in the

outer prismatic layer, whereas fragments produced by the stone crab *Menippe mercenaria* show shear fracture surfaces (Kosloski, 2011).

Implosion of nautiloid shells is suggested to occur due to increasing hydrostatic pressure during post-mortem sinking of the shell (Kanie et al., 1980; Saunders and Wehman, 1977; Ward and Martin, 1980) if the chambers retain some gas and are negatively buoyant (Maeda and Seilacher, 1996). Similarly, implosion may have occurred in ammonites, and the resultant fragments may resemble those produced by large durophagous predators (i.e., sharks, Mesozoic marine reptiles). Fossil cephalopod fragments attributed to implosion are few, most likely because most sedimentary rocks containing fossil cephalopods were deposited at shallower depths than those at which *Nautilus* shells implode (depths below ~300–800 m; see references above).

Multiple studies have shown differences between fragments produced by predators and those caused by other types of breakage. Fragments with angular margins are commonly attributed to fishes and crabs (Cintra-Buenrostro, 2007; Salamon et al., 2014), whereas tumbling experiments involving mollusk shells typically do not produce such angular fragments but instead yield more abraded, rounded shell pieces (Cintra-Buenrostro, 2007; Oji et al., 2003; Salamon et al., 2014) (Fig. 6). Field studies support these experimental data. For example, Leighton et al. (2016) found that sharp mollusk fragments are much more abundant at localities in which more durophagous predators were observed than at low-predation sites in British Columbia, Canada. Crab-induced damage to bivalve shells represented by peeling and nibbling traces along shell margins differed from damage induced by tumbling experiments, in which mechanical breakage also occurred away from the margin and the resulting damage pattern was more ragged (Cintra-Buenrostro et al., 2005). Trampling of shells by humans, possibly an analog for other animals walking on the sea bottom or along the shoreline, can also result in angular fragments, but only 20% of such shells could be confused with crab damage (Cintra-Buenrostro, 2007). Nevertheless, sharp-edged fragments produced by predators may be rounded over time by abrasion (Cintra-Buenrostro, 2007), which occurs most rapidly in the surf zone (Driscoll, 1970). Similarly, transport-induced breakage and abrasion to shells would lead to the preservation of

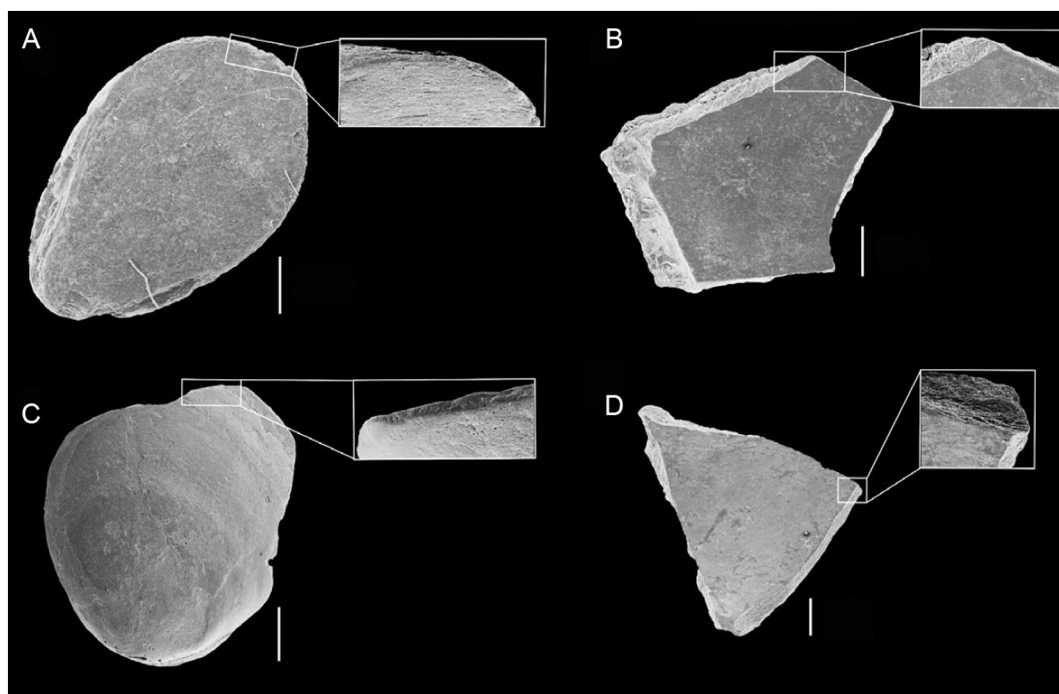


Fig. 6. Abiotic- (A and C) and biotic-induced (B and D) damage in shells. Rounded fragments after a tumbling experiment (A) and from the Baltic Sea surf zone (C). Angular fragments from a locality where fish and bivalves were observed to interact (B), and from the Carboniferous (Mississippian) of the Holy Cross Mountains, Central Poland (D). Insets show details of shell margins. Scale bars are 1 mm. Figure modified from Salamon et al. (2014: fig. 1C–F).

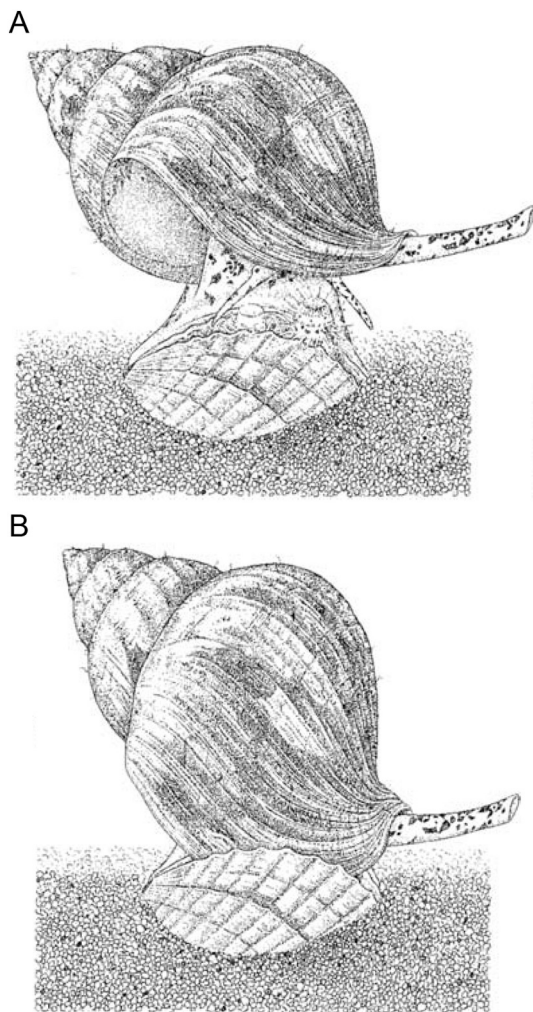


Fig. 7. The whelk *Buccinum undatum* mounts (A) and then attempts to chip the shell of the bivalve *Cerastoderma edule* by first inserting its outer lip between the valves (B). From Nielsen (1975: fig. 1).

only the most durable parts, whereas damage by predation would lead to a higher fidelity of the death assemblage (Cadée, 1994).

In the case of non-benthic mollusks such as some cephalopods, additional abiotic causes of fragmentation are possible. For example, collision of experimentally floating *Nautilus* shells with other objects caused apertural damage only during storms and probably resulted from impacts of *Nautilus* shells against the cage edge rather than due to collisions between shells (Wani, 2004). Although floating of *Nautilus* shells is rare (Mapes et al., 2010), extensive damage to shells transported to shallow waters by storms (Hembree et al., 2014) is possible. However, this damage is unlikely to be confused with predatory damage to the aperture or the ventral side of the shell.

In contrast to mollusks, distinguishing between biotic and abiotic damage in echinoid tests may be challenging because cross-plate fractures can result from both predation and physical agitation, as shown by tumbling experiments (Kidwell and Baumiller, 1990). Tumbling experiments represent extreme conditions of storms or intertidal environments (Driscoll, 1967) that do not apply to all sedimentary regimes in which echinoids live. Many predators of echinoids leave ambiguous damage that may be confused with abiotic damage (Grun, 2016; Kowalewski and Nebelsick, 2003; Sievers and Nebelsick, 2018), but no detailed study has compared biotic traces with abiotic damage thus far. For trilobites, it is difficult to distinguish the shape of damages attributed to predation/scavenging versus abiotically broken sclerites (Pates et al., 2017).

In sum, shell damage with a biotic origin can be distinguished from abiotic damage in many cases. Thus, changes in the frequency of damage through time may be meaningful. In particular, shifts through time in the type of fragments dominating fossil assemblages can be useful in tracking changes in the intensity of durophagous predation (e.g., Oji et al., 2003).

3.1.3. Non-lethal damage

Non-lethal damage on the exterior of a shell is often attributed to failed durophagous attacks (Alexander and Dietl, 2003; Gahn and Baumiller, 2005; Kröger, 2002; Vermeij et al., 1981), but predation by whole-animal ingestion can also produce non-lethal damage if the prey survives passage through the digestive tract of the predator (Cadée, 2011). Various shell breakage morphologies have been attributed to predation on mollusks (Alexander and Dietl, 2003), but non-lethal damage may also be self-inflicted, as shown by whelks preying on bivalves (Dietl, 2003a, 2003b; Nielsen, 1975) and by bivalves burrowing into shell hash (Alexander and Dietl, 2001a). Both extant and Neogene deep-burrowing bivalves contain repairs of breakage that cannot be attributed to predation (Alexander and Dietl, 2005; Checa, 1993); instead, such breaks formed during burrowing. In addition, diverse abiotic factors can produce non-lethal shell damage, including rolling rocks (Bulkley, 1968; Cadée, 1999; Raffaelli, 1978; Savazzi, 1984a, 1984b; Shanks and Wright, 1986) and moving ice (Cadée, 1999; Harper et al., 2012). In this section, we discuss methods to determine reliably whether non-lethal damage resulted from predation, non-predatory biotic causes, or abiotic causes.

Whelk gastropods use their thick outer lips to chip or wedge open the shells of bivalve prey (Fig. 7), thereby often damaging their lips (Dietl, 2003a, 2003b; Nielsen, 1975). This type of damage appears less jagged, is located more often at the mid-part of the lip or last growth episode, and shows less relief at the repaired fracture compared to evidence of crab-induced predation on the whelk *Sinistrofulgur* (Dietl, 2003a). Triangular divots (triangular depressions in the valve where the shell was removed) on the posterior margin of shallow-burrowing bivalves are interpreted as evidence of predation by siphon-nipping fishes and shore birds, whereas such damage found anteriorly on deep infaunal bivalves is harder to attribute to a specific predator (Alexander and Dietl, 2003). However, for the same shallow-burrowing bivalve species, Alexander and Dietl (2001a) reported an apparently self-inflicted triangular divot on a ventral-posterior position, likely caused by burrowing into shell hash. Experiments with bivalves further showed that triangular divots can form due to burrowing (Checa, 1993). Thus, divots cannot be attributed unequivocally to predation, although they seem to occur more frequently in shallow-burrowing or epifaunal bivalves (Alexander and Dietl, 2005) for which predation intensity may be higher.

Checa (1993) showed a variety of repair scar types in deep-burrowing extant bivalves from Spain. This non-lethal damage is unlikely to be caused by predators because of (1) damage morphologies said to differ from predatory damage, (2) anomalously high repair scar frequencies compared to scars attributed to predation in general, (3) shell fragments that are retained in the shell, and (4) the fact that deep-burrowing bivalves are less accessible to predators. Subsequent work on Neogene bivalves from the USA (Alexander and Dietl, 2005) confirmed that those repair scars were different from repairs of damage by predators. Alexander and Dietl (2005) added that the repair scars occurred only late in life, when specimens burrowed deeper, and that the scars were found mostly on the anterior portion of the shell, which is poorly accessible to predators. Rather, more likely causes of non-lethal breakage in deep burrowers include burrowing to avoid predators and sediment overburden or erosion during storms (Alexander and Dietl, 2005; Checa, 1993). Non-predatory breakage can also result from trapping of particles between valves, colliding with hard objects, and sediment loading (Alexander and Dietl, 2005). Experiments indeed show that damage along the commissure, especially posteriorly, can

form through burrowing (Checa, 1993). Scar shape, scar position on the shell, burrowing behavior, life habit, estimated storm frequency, and predatory activity in the studied unit are useful in assessing whether scars in burrowing bivalves are non-predatory in origin (Alexander and Dietl, 2005).

Semi-infaunal and epifaunal bivalves face the threat of other non-predatory damage such as impacts by ice and rocks, but the resultant traces often differ from biotic traces. Unlike damage to shells by predators, breakage of bivalve shells attributed to moving ice was positioned away from the shell margin, was present in one valve only, and did not result in shell loss (i.e., pieces were retained; Harper et al., 2012). Iceberg scour also may cause sediment particles to become trapped between calcium carbonate shell layers (Harper et al., 2012), a phenomenon not known to be caused by predatory attacks. Moreover, shell-crushing predators are rare to absent in modern polar marine ecosystems in which bivalves are subject to ice damage (Cadée, 1999; Harper et al., 2012). Experiments mimicking impacts of wave-borne rocks on limpets showed that breakage patterns differed among species and included chipping of the shell edge, spalling of the anterior shell, or collapse of the apex (Shanks and Wright, 1986). However, these damage patterns are similar to those reported in laboratory experiments involving crabs attacking three limpet species (Tyler et al., 2014), but detailed comparisons have not been performed so far. Damage induced by ice and rocks is restricted to certain types of environments and should not affect most assemblages preserved in the fossil record.

Much less has been published on taxa other than bivalves and gastropods. Regenerated crinoid arms are typically interpreted as records of non-lethal predatory attacks (Syverson et al., 2018, and references therein). Crinoids are resistant to wave stress or transport (Baumiller 2003b; Gorzelak and Salamon, 2013; Meyer, 1985) and purposeful shedding of body parts (autotomy) may happen under high abiotic stresses (oxygen deficiency, tumbling, temperature change, hypersalinity) or in the presence of predators (Oji and Okamoto, 1994). Autotomy may have also occurred in Devonian ophiuroids with damage possibly resulting from an attempt to dig out from a storm event bed (Reid et al., 2019), although cases when autotomy likely records a response to predators have also been reported (Fell, 1966). Non-lethal shell breakage in ammonoids and nautiloids is typically linked to the activities of predators (Kerr and Kelley, 2015; Klug, 2007; Kröger, 2002, 2004; Mironenko, 2017).

Holes that do not fully penetrate the shell are usually attributed to failed drilling predation by gastropods (e.g., Kelley et al., 2001). However, some incomplete circular holes may also be caused by other

processes, such as dissolution and pressure solution due to point contacts with other shells. Such holes are likely to be accompanied by additional holes, their placement on the prey skeleton may be more random, and their shape tends to be less circular than is typically observed for gastropod drill holes.

3.1.4. Correcting for abiotic damage

Despite challenges in differentiating abiotic and biotic damage, some research has moved forward by excluding inferred taphonomic breakage when estimating predation intensity. For gastropods, Vermeij (1982a) proposed to use the proportion of drilled shells that were broken to quantify post-mortem breakage, because breakage of such shells would have occurred after the death of the animal by a drilling predator. To obtain a frequency of lethal breakage (F_B) by durophagous predators, Vermeij (1982a) proposed the following formula:

$$F_B = \frac{N_B}{N} \times \left(1 - \frac{N_{BD}}{N_D}\right)$$

where N_B is the number of broken shells, N is the total number of shells (drilled + non-drilled), N_{BD} is the number of broken drilled shells, and N_D is the number of drilled shells. Vermeij's analysis was modified and named Vermeij Crushing Analysis by Stafford and Leighton (2011). They identified different types of damage in gastropods and compared the percentages of these types for drilled versus non-drilled shells. The difference per species represents the Estimated Crushing Mortality (ECM) (Stafford and Leighton, 2011):

$$ECM = \left(\frac{N_{BND}}{N_{ND}} - \frac{N_{BD}}{N_D}\right)$$

where N_{BND} is the number of broken non-drilled shells, N_{ND} is the total number of non-drilled shells, and N_{BD} and N_D are abbreviated as above. This method was subsequently used, for example, to calculate lethal breakage for bivalves from the late Cenozoic of Florida (Mondal et al., 2014; Mondal and Harries, 2015). Both methods assume that death from drilling made drilled individuals unavailable to durophages as prey; however, these prey may not have been drilled yet when the durophages were present and therefore were available to crushing predators. We here propose the Predatory Breakage Frequency (P_{BF}) for this scenario (Fig. 8):

$$P_{BF} = \frac{\left(\frac{N_{BND}}{N_{ND}} - \frac{N_{BD}}{N_D}\right) \times N_{ND}}{N}$$

Abbreviations are specified above. The P_{BF} can be used for

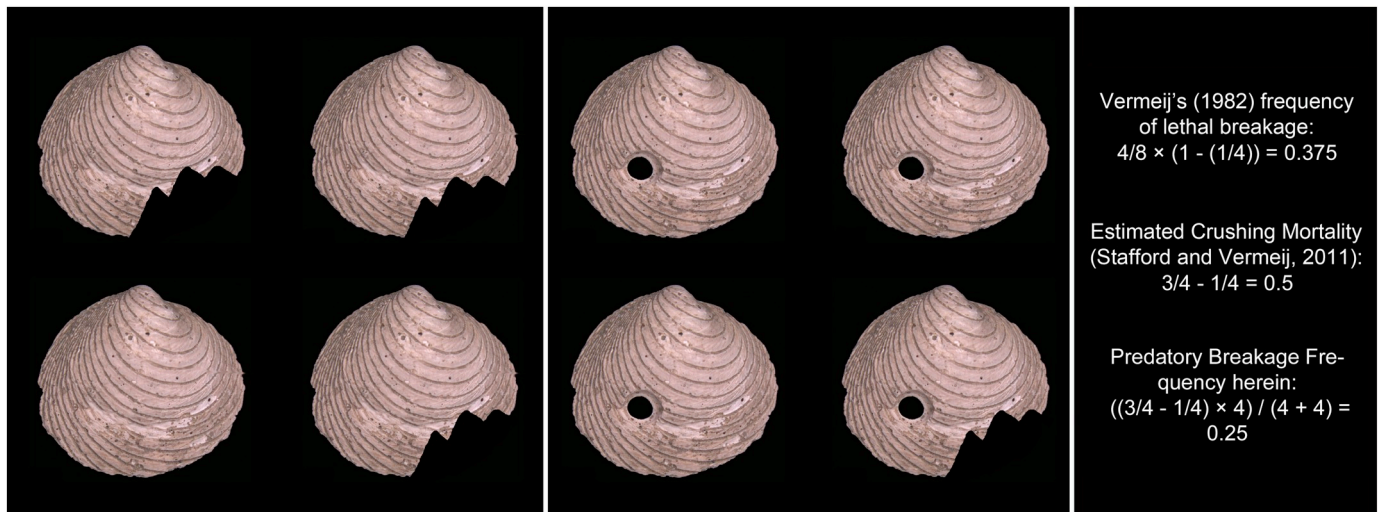


Fig. 8. Methods to account for taphonomic breakage by using broken drilled shells to obtain a predatory breakage frequency. For this example, one valve is presumed to represent one specimen. Specimen image modified after Klompmaker (2009: fig. 2A).

individual species of interest, for an entire assemblage, and for every species within the assemblage individually (if all taxa are drilled) and then weighted for the abundance of each species to estimate the P_{BF} . The ECM and P_{BF} may be seen as extreme endmembers that provide a range of likely lethal breakage intensities. All methods are based on the following assumptions: drilled shells do not break more easily than non-drilled shells (e.g., Kelley, 2008), broken shells have the same preservation potential as complete shells, hermit crabs have not preferentially reused undamaged gastropod shells (but see Hazlett, 1970), all specimens were collected regardless of the quality of preservation, fragments and drilled shells have not been preferentially transported into or out of the studied assemblage (Lever et al., 1961, for a beach setting), mistaken attacks on shells that were already preyed upon have not occurred (Kelley et al., 2001, for rare multiply drilled shells, which might indicate mistaken predation), specimens with a complete drill hole were dead and not in the process of starting to repair the drill hole (e.g., Robinson, 2014), and holes represent predatory drill holes (see Section 3.2 for criteria). The three methods are most straightforward to use for the single-shelled gastropods, but the fact that bivalves consist of two valves needs to be taken into account (i.e., a drill hole in one valve of a specimen is usually lethal, whereas durophagous breakage may be expected to affect both valves).

As for predatory breakage frequencies, drilling intensities can also be affected when post-mortem breakage is not taken into account. Often, only complete fossil specimens are used to quantify the frequency of predatory drill holes, whereas fragments are disregarded (but see Klompmaker, 2009). If fragmentation happened post-mortem and specimens with and without drill holes were equally likely to be fragmented across all taxa, no correction is needed. However, many marine predators are durophagous and can also destroy prey skeletons. In such cases, the surviving subset of complete skeletal remains can be severely biased. For example, the frequency of drilled specimens will be inflated, because the fossil record does not include potential prey destroyed by durophagous predators. To illustrate this issue, suppose that 1000 gastropod prey were present at a given site and 200 were killed by drilling (yielding a true drilling intensity of 20%). In addition, 400 were killed, and their shells were damaged beyond recognition, by durophagous decapods and/or fish. In this example, 600 specimens would remain to be preserved in the fossil record, of which 200 bear drill holes (yielding an observed drilling intensity of 33%). This issue was first recognized explicitly by Vermeij (1980). Recently, a more formalized approach was proposed and illustrated with examples (Smith et al., 2019), also taking into account post-mortem breakage.

3.2. Predatory versus parasitic traces

Studies of predation need to distinguish traces made by predators from those produced by parasites. Among trace fossils, morphologically similar drill holes are produced by several clades in both groups. Predatory and parasitic drill holes are particularly challenging to differentiate when found in assemblages that include both parasitic and predatory drillers and also in the early Phanerozoic when representatives of modern driller groups were absent (Table 2). Many studies have attempted to differentiate the two types of culprits with varying levels of detail (Ausich and Gurrola, 1979; Baumiller, 1990, 2003a; Baumiller et al., 1999; Brett, 2003; Daley, 2008; Hoffmeister et al., 2003; Kier, 1981; Klompmaker et al., 2016a; Kowalewski, 2002; Kowalewski et al., 2000; Leighton, 2001; Nebelsick and Kowalewski, 1999; Schimmel et al., 2012). We recognize the following 16 distinguishing criteria (see also Table 3):

- (1) Both drilling predators and parasites can produce multiple drill holes per shell (e.g., Brown and Alexander, 1994; Hutchings and Herbert, 2013; Kelley et al., 2001; Warén et al., 1994). Because interactions between hosts and parasites should not be lethal, a victim may be attacked by another driller, at the same or later time. In contrast, an attack by a predator usually leads to the death of the animal and thus only one drill hole is produced. Therefore, shells with multiple drill holes should more commonly record parasitic attacks. For example, the predatory cassid gastropods usually drill one hole per echinoid test today (Nebelsick and Kowalewski, 1999; but see Złotnik and Ceranka, 2005, for multiple inferred Miocene cassid drill holes per test), whereas parasitic eulimid gastropods often penetrate the echinoid test multiple times (Kowalewski and Nebelsick, 2003; Warén et al., 1994). Although rare, multiple platyceratid gastropods, often interpreted to be parasitic, have been found on crinoids (Baumiller, 2002). The frequency of multiple drill holes may differ depending on the prey: multiple drill holes per shell produced by the predatory octopods are common in *Nautilus* (30% of drilled shells; Saunders et al., 1991) but less so in mussels (1% of drilled shells; Nixon, 1979).
- (2) Healed or repaired drill holes should be much more common for parasites than for predators. During the long-term interaction between parasite and host, the parasite may get dislodged, after which the hole can be repaired. Healing is known for holes made by modern parasitic eulimid gastropods (Warén et al., 1994; Warén and Crossland, 1991) and most likely by a parasitic capulid gastropod (Orr, 1962). Healed drill holes, which can show a blister on the inside of the shell, are also known from the fossil record (Ausich and Gurrola, 1979; Baumiller and Macurda, 1995; Klompmaker et al., 2015; Robinson, 2014; Smith et al., 1985). However, healed holes can also occur following failed predation attempts, if the predator was interrupted (e.g., by its own predator or prey movement) after penetrating the shell but before killing the prey (Kitchell et al., 1986).
- (3) The location of drill holes relative to the prey's internal anatomy can give important clues about the type of driller. A drill hole that is located above the soft tissue (e.g., Chattopadhyay and Dutta, 2013; Hoffmeister et al., 2003; Klompmaker, 2011; Klompmaker et al., 2015; Leighton, 2001) is likely caused by a predator. If the hole is not located near the visceral mass (Baumiller et al., 1999), a parasite driller may be more likely.
- (4) Drill-hole size of predators, as a proxy for predator size (Klompmaker et al., 2017), frequently has been reported to be significantly positively correlated to prey size to maximize energy intake (Grun et al., 2017; Kitchell et al., 1981; Klompmaker et al., 2015; Kowalewski, 2004). Conversely, little evidence of significant positive correlation between drill-hole size and host size has been found for parasitic drillers (no significant correlation (Baumiller, 1993, 1996; Orr, 1962), and a weak significant correlation (Baumiller and Macurda, 1995)). This result is not surprising because parasites only rely on a portion of the food of their host, implying that the size of the host is less critical to meet the food requirements of parasites.
- (5) Predatory drillers tend to be larger than their prey, facilitating prey subjugation. On the other hand, parasites are usually smaller than their host. As a consequence, parasite-host body size ratios tend to be < 1 , whereas predator-prey size ratios are usually > 1 (Klompmaker et al., 2017; fig. S18).
- (6) As drill hole size and body size are positively correlated across drillers (Klompmaker et al., 2017), drill holes are expected to be smaller for parasitic drillers relative to predatory drillers for equal-sized prey/hosts.
- (7) As interactions between predators and their prey are brief, only rarely are predators preserved in the act of predation in the fossil record (exceptions: Blake and Guensburg, 1994; Boucot, 1990: p. 179). We do not know of a fossilized instance of a predatory driller atop a prey. Parasites are expected to be found more often attached to their host. Multiple examples have been found of extinct platyceratid gastropods, inferred to have been parasitic drillers of at least echinoderms (Baumiller, 1990, 1996, 2003a) and brachiopods (Deline et al., 2003), preserved on top of their

Table 2
Extant and fossil marine predatory and parasitic drillers and their stratigraphic ranges. PBDB = Paleobiology Database (<https://paleobiodb.org>).

| Phylum | Class | Family (Genus species) | Life habit drillers | Known stratigraphic range for taxon with lowest taxonomic rank (3rd column) | Reference(s) stratigraphic range | Reference(s) documenting drilling habit of taxon |
|-----------------|----------------|---|----------------------------|---|--|--|
| Mollusca | Gastropoda | Buccinidae (<i>Cominella</i> spp.) | Predatory | Paleocene – Recent | PBDB | Larcombe (1971); Peterson and Black (1995); Stewart and Creese (2004) |
| Mollusca | Gastropoda | Capulidae (<i>Capulus danieli</i> (= <i>Capulus sycophanta</i> & <i>Capulus dilatatus</i>)) | Parasitic | ?Pleistocene – Recent | Matsukuma (1978) | Bromley (1981); Kosuge and Hayashi (1967); Matsukuma (1978); Orr (1962) |
| Mollusca | Gastropoda | Cassidae (various genera) | Predatory | Cretaceous – Recent | Beu (2008); PBDB | Grun (2017); Hughes and Hughes (1971, 1981); Nebelsick and Kowalewski (1999) |
| Mollusca | Gastropoda | Eulimidae (various genera) | Parasitic | Cretaceous – Recent | Kier (1981); Neumann and Wisshak (2009) | Kosuge (1971); Schiaparelli et al. (2007); Warén (1981); Warén et al. (1994); Warén and Crossland (1991) |
| Mollusca | Gastropoda | Marginellidae (<i>Austroginella</i> spp.) | Predatory | Miocene – Recent | Coover and Coover (1995); Harris (1987); Laseon (1957) | Ponder and Taylor (1992) |
| Mollusca | Gastropoda | Muricidae (various genera) | Predatory, some parasitic | Cretaceous – Recent | Barco et al. (2012); Merle et al. (2011) | Herbert et al. (2009); Kowalewski (2004); Matsukuma (1977); Morton et al. (2007); Palmer (1988) |
| Mollusca | Gastropoda | Nassariidae (various genera) | Predatory | Paleocene – Recent | Galindo et al. (2016); PBDB | Chiu et al. (2010); Morton and Britton (2002); Morton and Chan (1997) |
| Mollusca | Gastropoda | Naticidae (various genera) | Predatory, some omnivorous | Cretaceous – Recent | Kase and Ishikawa (2003) | Casey et al. (2016); Kingsley-Smith et al. (2003); Kitchell et al. (1981); Wiltse (1980) |
| Mollusca | Gastropoda | Okadaidae (<i>Vayssierra elegans</i>) | Predatory | Recent | – | Kabat (1990); Young (1969) |
| Mollusca | Gastropoda | Dotidae (<i>Doto coronata</i>) | Predatory | Recent | – | Lambert (1991) |
| Mollusca | Gastropoda | Platyseratidae (various genera) | Parasitic | Ordovician – Permian | Bowsher (1955); Sutton et al. (2006) | Baumiller (1990, 2003a); Baumiller et al. (1999); Baumiller and Gahn (2018); Gahn and Baumiller (2003) |
| Mollusca | Cephalopoda | Octopodidae (various genera) | Predatory | Cretaceous – Recent | Kröger et al. (2011); Strugnell et al. (2006) | Anderson et al. (2008); Arnold and Arnold (1969); Nixon and Macconnachie (1988); Runham et al. (1997) |
| Foraminifera | Globothalamina | Turritinidae (<i>Floresina amphiphaga</i>) | Parasitic | Recent | Walker et al. (2017) | Hallock et al. (1998); Hallock and Talge (1994); Nielsen et al. (2002) |
| Foraminifera | Globothalamina | Gibicidae (<i>Gibicides antarcticus</i>) | Parasitic | Pliocene – Recent | Walker et al. (2017) | Walker et al. (2017) |
| Foraminifera | Globothalamina | Rosalinidae (<i>Hyrrokin</i> spp.) | Parasitic | Pleistocene – Recent | Walker et al. (2017) | Walker et al. (2017) |
| Nematoda | | | Predatory | ?Cretaceous – Recent | Sliter (1971, 1975) | Douglas (1973); Kabat (1990); Sliter (1971, 1975) |
| Platyhelminthes | Rhabditophora | Callioplandidae (<i>Koinostylochus ostreophagus</i>) | Predatory | Recent | – | Woelke (1957); Yonge (1964) |

Table 3

Criteria to distinguish between parasitic and predatory activity, explained in more detail in the text.

| Characteristic | Parasitism | Predation |
|---|--------------------|--------------------|
| (1) Multiple drill holes | More common | Less common |
| (2) Healed or repaired drill holes (incomplete drill holes) | More common | Less common |
| (3) Drill site directly over soft tissue (positioning drill hole) | N | Y |
| (4) Drill-hole size and prey size correlated | Less likely | More likely |
| (5) Size of attacker relative to prey | Usually small | Usually large |
| (6) Average drill-hole size | Relatively small | Relatively large |
| (7) Attacker found on prey | More likely | Less likely |
| (8) Tight fit of attacker with prey | Y | N |
| (9) Attachment scars of attacker on prey | Possibly present | Absent |
| (10) Embedment structure of prey around attacker | Possibly present | Absent |
| (11) Evidence of long-term maintenance of drill hole | Possibly present | Absent |
| (12) Ecology of extant members of group | Parasitic | Predatory |
| (13) Amount of soft tissue of host/prey | Less | More |
| (14) Relative abundance of body fossils in assemblage | Abundant parasites | Abundant predators |
| (15) Drill hole morphology | Not beveled | May be beveled |
| (16) Maximum size of host/prey | May be smaller | May be larger |

echinoderm host (e.g., Baumiller, 1990, 1996, 2003a; Klussendorf, 1983).

- (8) A long-term association between parasite and host is expected to result in a tight fit between the shell of a parasite and its host, which is not the case for predator-prey interactions. Tight fits have been shown for platyceratids (e.g., Baumiller, 1990; Bowsher, 1955; Clarke, 1908; Keyes, 1888) and capulids (Orr, 1962).
- (9) Etching scars indicating long-term association of likely parasites with their host are known for Paleozoic platyceratids (Baumiller, 1990; Gahn and Baumiller, 2006; Keyes, 1888), ?Cretaceous – Recent capulids (Breton et al., 2017; Kabat, 1990; Matsukuma, 1978; Orr, 1962), and modern eulimids (Warén et al., 1994; Warén and Crossland, 1991).
- (10) Embedment structures of the echinoderm host around the parasite have been figured for eulimids (Neumann and Wisshak, 2009; Warén, 1981).
- (11) In some cases, long-term maintenance of the drill hole can be inferred, indicating parasitism as the most probable biotic interaction. Kier (1981) argued that the size of a Cretaceous echinoid could be inferred at the time drilling by a probable eulimid gastropod commenced. The production of new plates was halted after drilling when only 48 porepairs were present in the drilled petal. Echinoids with 48 porepairs in the same assemblage are 21 mm long, whereas the drilled echinoid has a length of 42 mm, implying that the drill holes were not lethal to the echinoid. This method may work only for echinoids.
- (12) The ecology of the driller itself, if preserved, can be deduced from the ecology of modern representatives if there are any (i.e.,

phylogenetic inference). If no modern representatives are known, which is the case for the Paleozoic and early Mesozoic, a morphology close to that of an extant parasite or predator may help to infer the life mode of the drill-hole producer (i.e., morphological inference; see Brett, 2003; Klompmaker et al., 2016a).

- (13) The amount of soft tissue of the prey provides an additional clue as to whether a given drill hole records an attack by a predator or parasite. Mollusks tend to possess more soft tissue than similar-sized brachiopods (Peck, 1993), so that a drill hole in a mollusk is more likely to be predatory than parasitic in nature (but see capulids). Conversely, drill holes in brachiopods have been variously interpreted (Baumiller et al., 1999, 2006; Daley, 2008; Harper and Wharton, 2000; Hiller, 2014; Rojas et al., 2017; Schimmel et al., 2012). Compared to mollusks, most crinoids contain little soft tissue (Baumiller, 2003a), and these echinoderms were infested by parasitic platyceratid gastropods in the Paleozoic (see above). In turn, the meaty platyceratid gastropods, rather than their crinoid hosts, may have been targeted by predators (Brett, 2003; Syverson et al., 2018).
- (14) Assuming that parasitic and predatory drillers preserve equally well despite their size differences (Klompmaker et al., 2017: fig. S18), the relative abundance of the two groups in an assemblage may provide clues as to the nature of the drill-hole producer.
- (15) Drill-hole morphology may be useful to some extent. Beveled drill holes with a parabolic cross-section (*Oichnus paraboloides*) are most often attributed to naticid gastropods (Kelley and Hansen, 2003), and we know of no modern parasitic drillers that make similar-shaped drill holes. Similar-shaped drill holes, not to be confused with holes in echinoderms that may have been partially caused by embedment (e.g., Brett, 1985), are also known from the Triassic (Fürsich and Jablonski, 1984; Klompmaker et al., 2016a) and the Devonian (Smith et al., 1985) when naticids had not evolved yet (Kase and Ishikawa, 2003; Klompmaker et al., 2016a). Unlike Cretaceous and Cenozoic drill holes, early Phanerozoic drill holes need to be interpreted more cautiously because, thus far, only platyceratid gastropods are known to drill in the Paleozoic (Baumiller, 1990), but drill-hole morphology varies (Brett, 2003; Klompmaker et al., 2016a).
- (16) Because parasites are a metabolic drain for the host, infested hosts can have a smaller average and maximum size compared to conspecifics that are not parasitized (Baumiller and Gahn, 2002; Gahn and Baumiller, 2003, for fossil crinoids; not the case for infested fossil decapods, pers. obs. AAK), although this interpretation may be confounded if castration occurs (O'Brien and Van Wyk, 1985). If prey have not reached a size refugium for a predator, at least the maximum size should be similar between individuals that were preyed upon and those that were not attacked. Hence, the maximum size of specimens of the same species drilled by a parasite may be smaller than those drilled by a predator. Studies have yet to test this possible difference.

3.3. Identifying the predator

Once a fossilized predation event has been detected, the identification of the predator may be pursued. Theoretically, the taxonomic identification of a predator is possible for any type of predation indicator (e.g., direct indicators: trace fossils, gut contents, coprolites, preserved predation events; indirect indicators: taphonomic patterns, comparative anatomy; Kowalewski, 2002). Identifying the predator with high taxonomic resolution, however, can be quite difficult, particularly for trace fossils (e.g., Baumiller, 1993; Bromley, 1996), as detailed below. The probability of accurate identification at high taxonomic resolution depends on the type of evidence for and nature of a given predation event. Predators are most easily identified when preserved in the act of predation. Such fossils are rare, however, and constitute only a small percentage of predation-related fossils (Fig. 9;

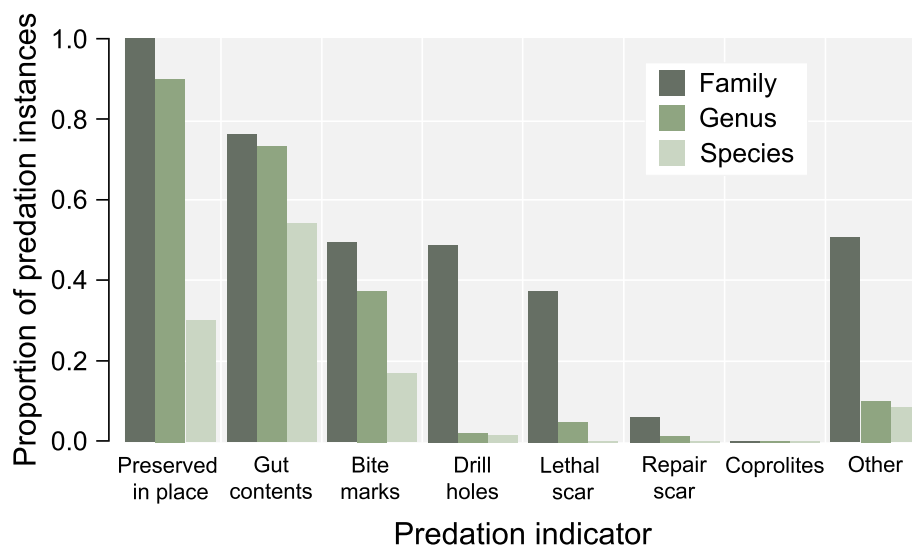


Fig. 9. The proportion of predation instances reported in published literature in which the predator was identified to the level of family, genus, and species for various indicators of predation: predation event preserved in place ($n = 10$; includes embedded teeth), gut contents ($n = 142$), bite marks ($n = 124$), drill holes ($n = 3321$), lethal scars ($n = 81$), repair scars ($n = 504$), coprolites ($n = 43$), and other ($n = 190$; includes irregular holes and other depressions, regurgitates, prey shell breakage, comparative anatomy, and organismal associations). A 'predation instance' was defined by the association of a predator consuming a particular prey taxon within a given study. The taxonomic resolution of prey varied across studies; the lowest taxonomic rank was used on a per case basis.

for exceptions see [Blake and Guensburg, 1994](#); [Boucot, 1990](#): p. 179). Similarly, fossils in which predators and their gut contents are preserved together often contain sufficient material to identify the predator to at least the family level, and often to the genus and species levels ([Fig. 9](#)).

Identifying the predator from trace fossils such as bite marks, drill holes, and lethal and repaired scars can be more difficult ([Fig. 9](#)). Such predation indicators often do not contain remains of the predator; rather they consist of evidence of predator activity preserved on fossilized prey skeletons. Numerous methods and criteria have been proposed to assist in identifying predators from such trace fossils. For example, bite marks on fossilized prey can be compared to preserved jaws or teeth of predators from the same assemblage (or nearby assemblages) to derive a comparative interpretation of predator identity (e.g., [Gorzalak et al., 2010](#); [Mapes and Hansen, 1984](#); [Neumann and Hampe, 2018](#)), and may be supported by experiments (e.g., [Neumann and Hampe, 2018](#)). The drill hole of a given drilling predator may be morphologically distinct (i.e., in shape) from that of other predators, allowing for reasonable identification of the driller through quantitative or qualitative analyses (e.g., [Dietl et al., 2004](#); [Dietl and Kelley, 2006](#); [Grey et al., 2005](#); [Kowalewski, 2004](#); [Paul and Herbert, 2014](#)), although drill-hole convergence (i.e. different predators making similar drill holes) does occur ([Klompmaker et al., 2016a](#)). Other types of traces that may be diagnostic include irregular holes and other depressions (e.g., stomatopod punctures; [Bałuk and Radwański, 1996](#); [Geary et al., 1991](#); [Pether, 1995](#)), and distinct prey shell breakage patterns (e.g., [Klompmaker et al., 2009](#); [Landman and Klofak, 2012](#); [Oji et al., 2003](#); [Takeda et al., 2016](#)). Of these additional types of traces, punctures are usually attributed to stomatopod predators, although crabs can also produce irregular holes (e.g., [Krantz and Chamberlin, 1978](#)). Various other attributes of a predatory trace (e.g., size selectivity and site stereotypy; [Leighton, 2001](#)) may be used to distinguish predators. Experiments comparing predatory traces of modern predators to those found in fossilized prey can also shed light on predator identities (e.g., [Dietl et al., 2004](#); [Pierrehumbert and Allmon, 2018](#)).

Recent technological advances can be adopted by paleontologists for identifying predators from trace fossils. For example, the advancement in 3D-imaging technology may allow for more precise descriptions of predatory traces in prey remains (e.g., Micro-CT and X-Ray imaging; [Kiel et al., 2010](#); [Sutton, 2008](#); [Wisshak et al., 2017](#)) that can be linked to particular predators. For example, microrasp marks in the vertical walls of drill holes attributed to scraping by radular teeth of muricid gastropods have been recorded in modern and fossil shells ([Schiffbauer et al., 2008](#); [Tyler and Schiffbauer, 2012](#)). The patterns of

microrasp traces could be explored to further identify the predator.

Although multiple studies have attempted to specify criteria for identifying predators based on trace fossil evidence, identification of predators is not trivial. Such techniques can sometimes reveal predator identity with high taxonomic resolution (e.g., species level: [Li et al., 2011](#); [Martinell et al., 2012](#); [Morton and Harper, 2009](#)), especially when multiple methods are employed at the same time ([Dietl et al., 2004](#)). However, the current literature review ([Fig. 9](#)) suggests that identifying the predator below the family level is rarely possible for such indicators of predation, as a diverse range of potential predators can produce a given trace type. Thus, identifying a specific predator with high taxonomic resolution can be difficult for a given predation event (e.g., [Klompmaker et al., 2016a](#); [Leighton et al., 2013](#); [Pierrehumbert and Allmon, 2018](#)). For example, for the late Cenozoic, [Kubicka et al. \(2017\)](#) reported that predatory drill holes and holes produced by humans for body adornments tended to be located in similar positions on mollusk shells. The same predator may also leave different morphological traces across individual prey items ([Arnold and Arnold, 1969](#); [Bromley, 1970](#); [Wodinsky, 1969](#)). Taphonomic alteration of a predation trace after the predation event can also hamper predator identification (e.g., [Chojnacki and Leighton, 2014](#)). Further, changes in ocean chemistry can influence dissolution rates of empty mollusk shells (e.g., [Clements et al., 2018](#); [Waldbusser et al., 2011](#)) and potentially alter the morphology of a predation trace.

Alongside trace fossils of predatory activity preserved in the remains of prey, bromalites (fossilized digestive material, see [Section 3.1](#)) from predators can also be used to indicate potential predation. Bromalites include fossilized regurgitates, intestinal contents (cololites), stomach contents (gastrolites), or, more commonly, fossilized feces (coprolites). In bromalites, identifiable remains of particular prey species contained within the regurgitates or feces can be preserved (e.g., [Conway Morris and Robison, 1986, 1988](#); [Nedin, 1999](#); [Reboulet and Rard, 2008](#); [Salamon et al., 2012](#)). Identifying the producer of bromalites, however, is difficult unless bromalites are preserved in association with the predator. In the studies we analyzed, identification of the producer(s) of bromalites such as coprolites was unsuccessful below the phylum level for marine fossils ([Fig. 9](#)). This uncertainty is primarily due to the fact that fecal preservations are highly variable in space and time, and because the fecal remains of many animal taxa are highly similar in appearance, making predator identification with high taxonomic resolution highly unlikely ([Chin, 2002](#); [Northwood, 2005](#)). Various techniques can aid in the identification of bromalite depositors. For example, DNA analysis, combined with radiocarbon dating, has been used to determine the producer of bromalites ([Wood et al., 2012](#));

however, to our knowledge, such analyses remain elusive for marine bromalites.

Other evidence of predation in fossil assemblages can also be used to identify the predator, including comparative anatomy (Butterfield, 2002) and organismal associations (Brandt et al., 1995; Jensen, 1990; Schwimmer et al., 1997). Community structure and the abundance of preserved predators in a given fossil assemblage can also be valuable in identifying likely culprits of predation events when coupled with the type of predation indicator (e.g., Brachaniewicz et al., 2017; Ganić et al., 2016; Klompmaker, 2009). Nevertheless, below the level of family, the identity of most predators remains difficult to determine (Fig. 9).

3.4. Recognizing and interpreting failed predation

For the purposes of this section, we define failed predation as instances in which an attack did not result in the death of the prey, although the attack might be considered successful from the perspective of the predator if soft tissue was obtained. In many predator-prey systems, failed predation might not leave an identifiable trace, especially when failure occurs during the early phase of an attack. However, once the predator makes a predatory trace on the prey's shell, the failed predation attempt can often be identified for both drilling and durophagous predation. In the case of vertebrate bite marks in large and robust prey, it can be difficult to determine whether a bite was lethal. However, if the anatomy of the prey is known, the location of the bite mark can indicate whether a bite was likely to have been fatal (e.g., Bianucci et al., 2010). The most common types of failed predation in the fossil record are represented by incomplete drill holes and repair scars in marine invertebrate shells. Repaired holes, healed crinoid arms, and regenerated bone (Fig. 10) are also known from the fossil record. Other types of failed attack are items that are mistakenly perceived as prey (Gaemers and Langeveld, 2015) or shells that are already empty but were attacked nevertheless (Walker and Behrens Yamada, 1993).

Incomplete drill holes are those that do not penetrate the entire

thickness of the shell of the prey, precluding access by the driller to the prey's soft parts. An incomplete hole is often accompanied by a central boss on the bottom of the drill hole for naticid gastropod drillers (e.g., Kabat, 1990). Some workers (see review by Visaggi et al., 2013) have argued that incomplete holes need not represent failed predation; a bivalve prey that is suffocated may gape, allowing the predator to feed without completing the drill hole. However, prey suffocation reported in the literature usually can be attributed to poor prey health or other laboratory effects (Visaggi et al., 2013) and is unlikely to be common in natural environments. Penetration of the shell by a drill hole does not necessarily mean that predation was successful, as Kitchell et al. (1986) have argued that drill holes are not functional when the ratio of inner drill hole diameter to outer drill-hole diameter is < 0.5 for naticid drillers.

Several methods have been used to quantify failed drilling predation. The most commonly used metric, prey effectiveness, was defined by Vermeij (1987) as the ratio of the number of incomplete drill holes to the total number of attempted holes (complete and incomplete). Hansen and Kelley (1995) calculated the percent of individuals with an incomplete drill hole. Similarly, Sawyer and Zuschin (2010) calculated an Incomplete Drilling Frequency as the number of incomplete drill holes divided by the number of prey individuals. Similar metrics could be developed for repaired drill holes, but such holes are likely to be too rare for metrics to be meaningful. The occurrence of multiple drill holes (whether complete or incomplete) has also been used to indicate failed drilling by naticid gastropods (Kelley et al., 2001), as prey with more than one drill hole survived an attack to be drilled again (Kitchell et al., 1986). Kelley and Hansen (1993) defined MULT as the proportion of drill holes in multiply drilled specimens.

Repair scars result when prey of a durophagous predator survive and secrete new shell material to repair the damage caused by the attack. Metrics for calculating repair frequency include the number of scars in a sample divided by the total number of specimens (scars per shell), the percent of individuals with repair scars (e.g., Dietl and

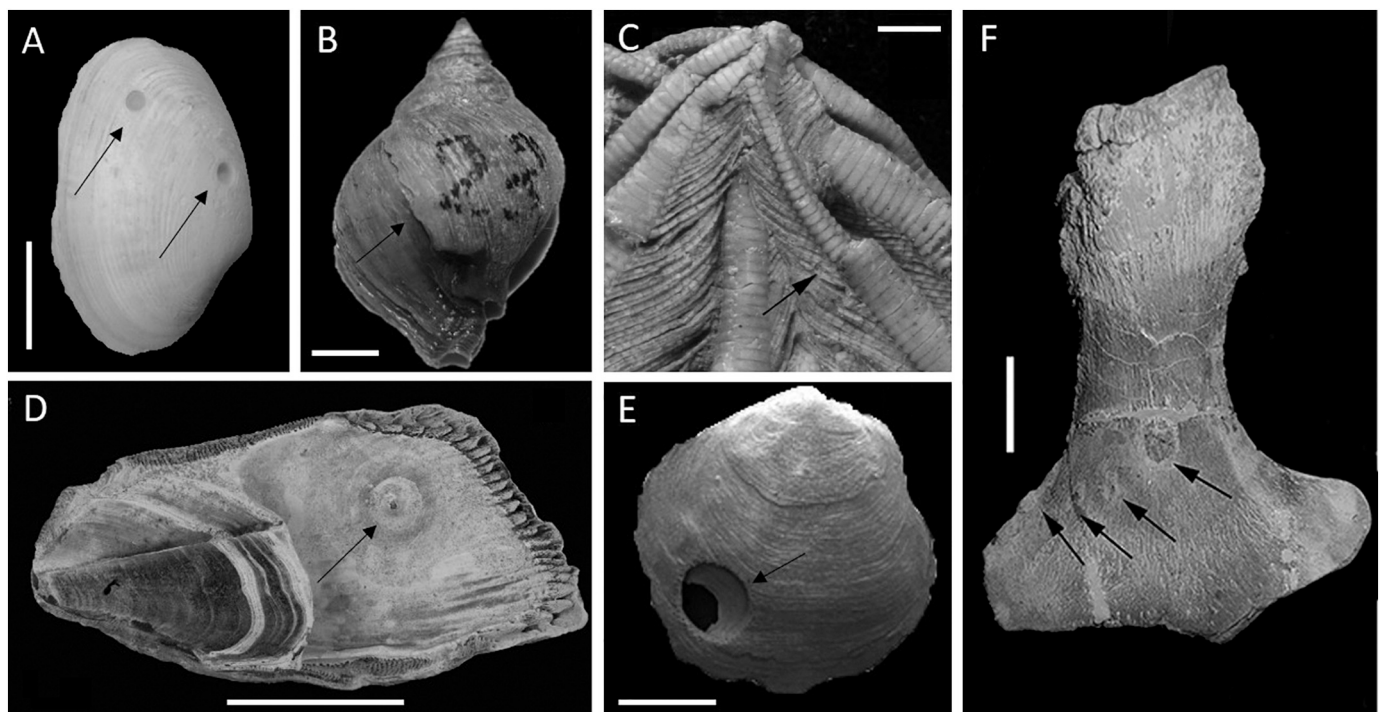


Fig. 10. Traces caused by failed predation, indicated by arrows. (A) Recent bivalve showing two incomplete drill holes, and (B) Recent gastropod with a repair scar developed after a durophagous attack, scale bars = 10 mm. (C) Examples of a regenerated arm in a Paleozoic crinoid (image courtesy: Forest J. Gahn), scale bar = 5 mm. (D) Repaired drill hole on the inside of a Miocene barnacle plate (modified from Klompmaker et al., 2015), scale bar = 10 mm. (E) Partially repaired drill hole on a Recent brachiopod shell (modified from Robinson, 2014), scale bar = 1 mm. (F) Example of a healed Middle Jurassic plesiosaur bone after an attack (modified from Rothschild et al., 2018), scale bar = 50 mm.

Kosloski, 2013; Lindström and Peel, 2010; Nagel-Myers et al., 2009, 2013), and the number of scars per shell surface area (Preston et al., 1993). These methods are useful in different situations; the percent of shells with scars most closely reflects selection pressure (Alexander and Dietl, 2003). Arm regeneration in crinoids has been quantified in a similar manner, i.e., as percent of individuals with at least one regenerated arm (Aronson et al., 1997; Baumiller and Gahn, 2003). Repair frequencies are often standardized by prey age (or size as a proxy of age) because older individuals accumulated repair scars over a longer period of exposure to durophagous hazards (Vermeij et al., 1981). Interpretation of the incidence of failed durophagous predation is challenging (Leighton, 2002); increases in repair frequencies can result either from more attacks or from decreased success of those attacks.

Interpretation of the causes of failed predation is far from simple. Failure may be related to the efficiency of the predatory group; for example, Vermeij (1982b) showed that muricid gastropods exhibit a higher incidence of failure in drilling compared to naticid gastropods. He attributed the incidence of failure in a prey population to the abundance and efficiency of predators in relation to the prey and the availability of other prey species. If predator abundance guides the incidence of failure, then the frequencies of successful and failed predation should be positively correlated. However, failure could also result from a behavioral change. For example, many muricids can switch from a drilling to a chipping/wedging strategy (e.g., Sawyer et al., 2009). In such cases, a correlation between successful and failed predation may not be obvious.

Failure of an attack also can be due to the effectiveness of prey-specific defenses. The concept of prey effectiveness as a measure of failure is based on the implicit assumption that the prey contributes to such failure, but prey abandonment by the predator can also be unrelated to prey traits. For example, abandonment can occur when the predator is physically interrupted (e.g., by a storm event) or by an external agent such as its own predator, referred to as a “secondary predator” (Kelley and Hansen, 2003). In fact, predatory or scavenging activities may be abandoned due to the mere presence of a secondary predator. For example, Atema and Burd (1975) demonstrated that the mud gastropod *Nassarius obsoletus*, a scavenger of crushed mollusks, abandoned scavenging in the presence of crushed conspecifics. Similarly, in an experimental study evaluating the non-consumptive effects of a durophagous predator on the drilling performance of muricids, Chattopadhyay and Baumiller (2007) demonstrated that the presence of a secondary predator could deter drilling predators and significantly increase the incidence of voluntary abandonment (see also Hutchings and Herbert, 2013). A strong negative correlation between the frequencies of drill holes that are complete and repair scars observed in the fossil record (Chattopadhyay and Baumiller, 2010) is consistent with those neontological experiments. The relationship between the percentage of successful and unsuccessful attacks may vary with the trophic level of the predator. The number of potential predators is fewer higher up the food chain, suggesting that disruption may occur less frequently. Thus, no strong relationship between successful and unsuccessful attacks is expected for apex predators. Chattopadhyay and Baumiller (2007) further demonstrated that the decision of abandonment is time dependent: drillers do not abandon their prey if they have invested a significant amount of time before being disturbed. In such cases, prey traits are likely to have contributed to failed drilling, in that prey with thicker shells require a greater time investment by the predator (Kelley et al., 2001).

3.5. Taphonomic and other factors affecting evidence of predation

Deductions about biotic interactions from drill holes and repair scars, two of the most informative predation traces, might not always be flawless. The tacit assumption for interpreting predation is that the quantitative data provided by traces of predation (e.g., frequency of traces, distribution of traces across prey species and prey size classes)

are not influenced by taphonomic or other factors. This section focuses on such factors, whereas Section 3.1 reviewed abiotic processes that can produce damage similar to predatory traces.

Holes produced by drilling predators may be affected by taphonomic factors (De Cauwer, 1985; Harper et al., 1998; Velbel and Brandt, 1989), including differential preservation and transport of drilled and undrilled valves. The presence of a drill hole in a valve may reduce the resistance to taphonomic forces before or after burial. Roy et al. (1994) found a significant difference in strength between drilled and undrilled bivalves; drilled valves were weaker in point-load compression experiments. This bias, however, appears only to affect shells in high-energy environments and may not have significant impact during natural sediment compaction (Hagstrom, 1996; Kelley, 2008; Nebelsick and Kowalewski, 1999; Zuschin and Stanton, 2001). Experimental fragmentation by sediment compaction using drilled and non-drilled gastropod shells of *Olivella biplicata* did not show elevated breakage of drilled specimens (Dyer et al., 2018), suggesting that compaction did not affect drilling intensity in this case. Nevertheless, criteria for determining the degree of taphonomic bias due to shell breakage and methods for reconstructing the original drilling intensity have been proposed for a few scenarios (Kaplan and Baumiller, 2000; Roy et al., 1994).

Differential transport of valves by currents or other agents may alter drilling frequency in both transported and lag assemblages. The hydrodynamic properties of a shell depend on a number of factors, including its size, shape, and composition. Several studies have examined current velocity required for entrainment and post-transportation alignment of shells of brachiopods (Alexander, 1975, 1984, 1986b; Johnson, 1957; Kornicker and Armstrong, 1959; LaBarbera, 1977; Menard and Boucot, 1951; Nagle, 1967; Quaresma et al., 2007; Savarese, 1994), bivalves (Allen, 1984; Brenchley and Newall, 1970; Chattopadhyay et al., 2013a; Frey and Dörjes, 1988; Futterer, 1982; McKittrick, 1987; Olivera and Wood, 1997; Trewin and Welsh, 1972), and micro-benthos (Ostracoda and Foraminifera; Kontrovitz, 1975; Kontrovitz et al., 1978; Kontrovitz and Snyder, 1981). Transport could alter drilling frequencies by preferential removal of a particular size class, shape class, or taxon from an assemblage. Minor differences in the geometry of opposing valves of a bivalved shell can result in different transportation patterns for the two valves, yielding a sorted assemblage. This phenomenon of preferential valve movement by currents has been reported for brachiopods and bivalves (Behrens and Watson, 1969; Boucot et al., 1958; Chattopadhyay et al., 2013a; Frey and Henderson, 1987; Kornicker et al., 1963; Lever, 1958; Lever and Thijssen, 1968; Martin-Kaye, 1951; Nagle, 1964). If predators preferentially drill one valve, as discussed below, differential transport of valves might alter the true drilling frequency.

Additionally, drilling frequency can be affected by hydrodynamic differences between drilled and undrilled shells. A number of experimental studies have demonstrated that drilled shells entrain at lower velocities than undrilled shells of the same species (Chattopadhyay et al., 2013b; Lever et al., 1961; but see Molinaro et al., 2013). Chattopadhyay et al. (2013b) also demonstrated that the position of the drill hole dictates the entrainment velocity, implying possible sorting based on stereotypic drill-hole site selection by the driller. In explaining differential levels of predation in Cretaceous oysters from Utah, USA, Tapanila et al. (2015) argued for transport-driven mixing; two spatially separated oyster populations that experienced different levels of predation pressure produced a mixed assemblage due to post-mortem transport.

In addition to the effects of differential transportation, unequal preservation of valves can influence measured drilling frequencies. Differences in shape or thickness of two valves of a specimen (a very common phenomenon for brachiopods as well as some groups of bivalves such as Corbulidae) may lead to an unequal preservation probability of the valves (Velbel and Brandt, 1989). Preferential removal of a specific valve might change the original drilling frequency (Kaplan

and Baumiller, 2000) if valves are drilled at different frequencies. Valve preference by drillers is not very common for equivalved prey but may occur for inequivalved taxa, such as corbulid bivalves (e.g., De Cauwer, 1985; Kardon, 1998; Kelley, 1988; see Section 5). Furthermore, shell preservation can be influenced by chemical factors, possibly leading to different preservation potentials at different times (see Sections 4.5 and 4.6). For example, Clements et al. (2018) showed that higher levels of seawater CO₂ (800 and 4000 μ atm) resulted in variably increased shell loss due to dissolution (0 to 7%) for the gastropods *Littorina littorea* and *Euspira heros*. Preferential shell dissolution of taxa due to their shell composition may alter the predation record, if the predation record of those groups significantly deviates from that of more durable species.

Drilling frequencies may also be affected when non-drilling durophages work as taphonomic agents. Drilling frequencies are calculated relative to the total number of shells (drilled and undrilled) in an assemblage. However, if durophages obliterate undrilled shells by crushing, the proportion of drilled shells in an assemblage will be inflated (Vermeij et al., 1989). This problem is most severe when a large fraction of prey specimens was destroyed by durophages (Smith et al., 2019) and they are not accounted for when calculating drilling intensity (see Section 3.1.4).

Factors other than the taphonomic aspects mentioned above may also affect the drilling and durophagous predation records. For instance, the effect of shell morphology on the visibility and the preservation of a repair scar may potentially influence the inferred repair scar frequency. Sime and Kelley (2016) observed an apparent difference in the number of repair scars between two species of the bivalve *Glycymeris* with strikingly different ornamentation. The species with relatively narrow ribs accumulated a higher number of small fractures that could be considered as repair scars; however, fractures of equal severity would not be as recognizable if found on the species with broad ribs. Similarly, Forcino et al. (2017) suggested that repair scars may be more readily visible on finely ornamented brachiopod taxa than in taxa without ornament. Also, some repair scars that are not visible on the shell surface can be seen in a cross-section of the shell (Ramsay et al., 2001).

Sampling and subsequent processing protocols may also affect the inferred drilling intensity. Surface sampling conducted in grids for lithified rocks resulted in a lower observed drilling percentage compared to the actual percentage because shells are not completely exposed (Chattopadhyay and Bala, 2013). Bulk sampling of unlithified materials, although unaffected by this bias, may still show biases that are introduced during processing. The effects of size filtering (through sieving) on studies of drilling predation may be quite important. A severe bias may creep in through the sieving protocol if the predators exhibit size-specific selection of prey and the study considers samples of only a specific sieve size (Kowalewski, 2002). If the size fraction considered for the study happens to be the preferred size class, observed drilling percentage may be unrealistically inflated; the reverse can occur when the preferred size class is missed by sieving. Nevertheless, only a handful of studies have examined the effects of size filtering on measured drilling intensities in detail (Chattopadhyay et al., 2016; Hattori et al., 2014; Hausmann et al., 2018; Kowalewski and Hoffmeister, 2003; Ottens et al., 2012; Visaggi and Kelley, 2015).

Another common practice that may affect drilling percentage is to consider only valves with complete or near-complete margins (Kosnik, 2005; Leighton, 2002). The effect of such a practice was demonstrated for Pliocene mollusk assemblages (Klompmaker, 2009); a significant increase in drilling intensity was observed when fragmented valves, broken by compaction, were included in the analysis, because specimens that were preferentially broken represented species that were commonly drilled. Likewise, preferential fragmentation of taxa that are rarely drilled would artificially inflate an assemblage drilling percentage. Within-species analyses using a Pliocene turritellid gastropod showed limited differences (Johnson et al., 2017).

Experience in the recognition of drill holes does not seem to

influence results on drilling predation. Using bivalves from Pleistocene unlithified sediments, Hattori et al. (2014) observed no significant differences in several predation estimates obtained by trained novice collectors versus veteran collectors.

Finally, the location of prey handling may influence drilling intensity. A recent study on drilling in modern echinoids has shown a 96.8% drilling intensity (Tyler et al., 2018). The authors argued that the predation mode of the cassid predator within the sediment enhanced the survival of drilled tests compared to echinoids that died due to other causes.

4. Environmental gradients

4.1. Depth gradients

Most aspects of the marine physical environment vary with water depth (see, e.g., Dodd and Stanton, 1990) – water energy, probability of disturbance, oxygenation, light penetration, primary productivity, temperature, salinity, nutrients, and the nature of the substrate (e.g., sediment composition, grain size, and texture). Because those factors also control the distribution, diversity, and abundance of species, community composition changes along a depth gradient (see, e.g., Carney, 2005; Sander and Lalli, 1982; Tyler and Kowalewski, 2014). Thus, predator-prey interactions can be expected to vary with depth as different combinations of predators and prey come into contact. Foraging strategies may vary with depth among closely related, morphologically similar species (Zintzen et al., 2013) as food resources change, and trophic structure differs between bathyal and shallower depths (Maxwell, 1988). Physical disruptions related to environmental energy also can affect the activities of predators, and environmental stress can reduce the abundance of predators (McClanahan, 1992); predator-prey interactions should be less important in structuring communities in physically stressful environments (Micheli et al., 2002). In addition, temperature affects metabolic rate and thus influences rates of predation and the lifespan over which prey are exposed to predators (Vermeij, 1987). To some degree, then, patterns of predation along depth gradients might be expected to mirror patterns along latitudinal gradients.

Investigations of the relationship of predation to depth, both in the modern environment and the fossil record, have used a variety of approaches (Table 4). Some studies have inferred the intensity of predation from the diversity, abundance, or density of predators. Stomach contents and, in recent years, isotopes have been used to interpret predator diets. Much of the work comparing the intensity of predation at different depths has used trace fossils and their modern counterparts. In particular, repairs following sublethal damage by durophagous predators and drill holes by shell-drilling gastropod and octopod predators have figured prominently in studies of depth gradients in predation. In other cases, lethal breakage, shell fragmentation, and regeneration of body parts have been used to explore variation in predation with depth.

Despite a growing body of data from both modern environments and the fossil record, the relationship between predation and depth is unclear. The diversity of predators is thought to be less in deep water today (Aronson and Blake, 2001; Harper and Peck, 2016), and the deep sea generally has been regarded as a refuge from predation. Vermeij (1987) argued that many taxa with defensively inferior architecture (e.g., echinoids with flexible tests, loosely coiled or umbilicate gastropods, and bivalves and gastropods with thin, unornamented shells) were once abundant in shallow waters but are now restricted to the deep sea. Perhaps the best-known example is the inferred post-Jurassic retreat of stalked crinoids to deeper waters (Baumiller and Gahn, 2003; Bottjer and Jablonski, 1988; Meyer and Macurda, 1977; Wisshak et al., 2009). Meyer and Macurda (1977) argued that the replacement of stalked crinoids by mobile, better-defended comatulids in waters < 100 m deep was due to increased predation in shallow waters from the late Mesozoic radiation of teleost fish. This conclusion was supported

Table 4

Studies that examine relationship of predation to water depth.

| Reference | Predation metric | Age & Taxon | Depth | Results |
|---|------------------|---------------------------------|---|---|
| Studies supporting decrease in predation with depth | | | | |
| Harper and Peck (2016) | RF | Recent brachiopods | 0–199, 200–999, > 1000 m | RF decreases w/depth; all samples w/RF > 0.105 from < 100 m |
| Dietl et al. (2000) | RF | Cretaceous–Paleocene oysters | Onshore vs offshore shelf | Onshore > offshore predation (3× for exogyrine, 2× for pycnodont oysters) |
| Walker et al. (2002) | Lethal breaks | Recent gastropods | Shallow shelf 15–30, outer 70, slope 100–267 m | Signif. more pred. at < 30 m than deeper; pred. on shelf > slope |
| Tomašových and Zuschin (2009) | DF & frag. | Recent brachiopods | Shallow shelf to basin (~1500 m) | Frag. decrease w/depth; decrease in DF w/depth ns |
| Oji (1996) | Arm regen. | Recent crinoids | 178 to ~500 m, ~500 m to 723 m | Regen. freq. for upper slope signif. > deeper (but ns using presence/absence of regen.) |
| Kiel (2010) | Abund. | Mesozoic & Cenozoic seep faunas | Deep (500–2000 m) vs shallow (16–900 m) | Predator abund. decrease w/depth in Cenozoic; % obligate seep taxa increase w/depth (Cenozoic & Mesozoic) |
| Amano et al. (2010) | Abund. | Miocene mollusks | Deep (1000–2000 m) vs shallower seeps | Deep seeps lack predatory gastropods; diversity lower & % obligate taxa higher |
| Zintzen et al. (2013) | Stable isotopes | Recent hagfish (predators) | 50–900 m | Shallow species = active predators; deeper species = scavengers (e.g., whale falls) |
| Studies indicating increase in or substantial predation at depth | | | | |
| Voight (2000) | RF | Recent vent limpets, tubeworms | Deep sea vents | Sublethal pred. common (e.g., on 73 of 74 tube worms) but lethal unknown |
| Walker and Voight (1994) | RF | Recent archaeo-gastropods | Bathyal (depths 300–1000 m for some samples) | High RF = 0.28–1.0 for <i>Bathybembex</i> (small samples), 0.68–0.91 for <i>Gaza</i> |
| Carriker (1998) | DF | Recent mollusks | Deep sea | Drill holes up to 2690 m, naticid gastropods as deep as 6860 m |
| Sawyer and Zuschin (2010) | DF | Recent mollusks | Intertidal vs sublittoral (4–15 m) | Intertidal DF (1.4%) < sublittoral (27.4%) |
| Zuschin and Ebner (2015) | DF | Recent mollusks | Intertidal vs shallow subtidal | Intertidal DF (1.2%) < shallow subtidal (25.7%) |
| Walker (2001) | RF & DF | Pliocene gastropods | mid to outer shelf & bathyal turbidites | RF = 0.25, DF = 0.32; 66% of species had repairs, 68% of species drilled |
| Maxwell (1988) | Trophic struc. | Miocene mollusks | Upper bathyal (~400–800 m) | Predators & deposit feeders dominant; few suspension feeders |
| Studies with mixed results or no pattern with depth | | | | |
| Rhoads et al. (1982) | RF | Recent mussels | Deep sea vents | 76% w/repairs, similar to shallow water |
| Vale and Rex (1988) | RF | Recent proso-branch gastropods | < 200, 200–1000, 1000–2000, 2000–4000, > 4000 m | Regression of RF or % species w/repairs vs depth ns, deep sea RF in range of shallow |
| Vale and Rex (1989) | RF | Recent rissoid gastropods | 500, 800, 1100 m | Median RF = 0.11 in range of shallow habitats, diff. among 500, 800, 1100 m ns |
| Kropp (1992) | RF | Recent mollusks | Inner shelf 90–91 m, outer shelf 145–161 m, upper slope 409–565 m | Prosobranch gastropods: upper slope RF < inner or outer shelf. Scaphopods: upper slope RF > inner shelf. Opisthobranch gastropods: diff. w/depth ns |
| Sander and Lalli (1982) | DF | Recent mollusks | 125, 175, 225 m (shelf-slope margin) | Avg DF = 0.163, 0.42, 0.30 for 125, 175, 225 m w/only signif. diff. between 125 and 175 m |
| von Rützen-Kositzkau (1999) | DF | Recent mollusks | Depths from 4 to 1898 m | DF greatest (up to 0.30) at < 350 m (especially for gastropods) and > 1000 m (especially for bivalves) |
| Hansen and Kelley (1995) | DF | Eocene bivalves and gastropods | Inner and middle vs outer shelf | No trend w/depth on inner & middle shelf; outer shelf DF (0.21) > inner to middle (0.08) |

(continued on next page)

Table 4 (continued)

| Reference | Predation metric | Age & Taxon | Depth | Results |
|-----------------------------------|------------------|---------------------------------|--|---|
| Hoffmeister and Kowalewski (2001) | DF | Miocene bivalves and gastropods | Sand vs clay facies in Boreal and Paratethys | Boreal: sand DF (0.28) > clay (0.15); Paratethys clay DF (0.19) > sand (0.13) |
| Sawyer and Zuschin (2011) | DF | Miocene mollusks | Intertidal vs sublittoral | Results vary with taxonomic level and Miocene stage; in Badenian intertidal DF (6.9%) < subtidal (9.3%) |
| Chattopadhyay et al. (2015) | DF | Recent bivalves | 0–52 m; shallow < 10, deep > 10 m | No signif. relation of depth to DF; shallow DF = 0.17, deep = 0.19, diff. ns |
| Chattopadhyay et al. (2014b) | EDF | Recent bivalves | 0–52 m; shallow < 10, deep > 10 m | Shallow EDF = 0.06, deep = 0.07, diff. ns |

Abbreviations: RF, repair frequency; DF, drilling frequency; signif., significantly; frag., fragmentation; regen., regeneration; freq., frequency; abund., abundance; ns, non-significant; struc., structure; diff., difference.

by Oji (1996), who found significantly greater arm regeneration in the extant stalked crinoid *Endoxocrinus parrae* at the upper slope than at deeper sites. Whether stalked crinoids migrated to deeper waters or already were present there is unclear because deep-water deposits are poorly known from the sedimentary record. However, some Triassic and Jurassic deep-water sediments contain stalked crinoids (Salamon and Gorzelak, 2010; Thuy et al., 2012).

Frequencies of shell breakage and repair provide additional evidence for the deep sea as a refuge from predation. Walker et al. (2002) tethered empty gastropod shells at shallow shelf, outer shelf, and slope sites along transects off the Bahamas. Slope samples experienced significantly less “lethal” breakage than did shells deployed on the shelf, with significantly more attacks on tethered shells at 15–30 m depth compared to deeper-water sites. In a study of extant brachiopods by Harper and Peck (2016), repair frequencies (RF) decreased significantly with depth; all samples with RF > 0.105 came from depths < 100 m, with sites deeper than 1000 m exhibiting RF < 0.03. The results of Dietl et al. (2000) also support the view that predation decreases with water depth; Cretaceous and Paleocene gryphaeid oysters exhibited two- to three-times greater repair frequencies in onshore than offshore sites, with a corresponding decline in shell-strengthening ornamentation with depth.

Nevertheless, other studies show no clear-cut pattern in intensity of predation with depth (Table 4). Vale and Rex (1988, see also Vale and Rex, 1989) found no significant relationship between depth and either repair frequencies or percent species with repairs for extant gastropods from depths < 200 – > 4000 m in the western North Atlantic; deep-sea RF were within the range of shallow-water samples. Inner shelf, outer shelf, and upper slope samples off California, USA, yielded different patterns in repair frequency with depth for different groups of mollusks (Kropp, 1992). Nor did Sander and Lalli (1982), sampling from the shelf-slope margin of Barbados, find a consistent trend in drilling predation with depth. In the Red Sea, predation by shell-drilling naticid and muricid gastropods was greatest at depths shallower than 350 m and > 1000 m (von Rützen-Kositzkau, 1999), with bivalve and gastropod prey showing slightly different patterns. Tomašových and Zuschin (2009) also did not find a significant relationship between drilling frequency (DF) on Red Sea brachiopods and depth (shallow shelf to basin), although fragmentation (in part due to predation) did decrease significantly with depth. Such work in the modern environment shows that predation can be intense at deep-water sites (see also Carriker, 1998; Walker and Voight, 1994).

Some work in the fossil record is consistent with the conclusion that intense predation can occur in deeper waters. Although Hansen and Kelley (1995) found no trend in DF along a depth gradient from the inner to middle shelf in the Eocene Moodys Branch Formation of Mississippi, USA (see below), drilling frequencies in the outer shelf Yazoo Formation were significantly greater than in the shallower Moodys Branch. Intense predation in deeper water is consistent with results

from Pliocene turbidite deposits of Ecuador that contained mid-to-outer shelf and bathyal gastropods; Walker (2001) found repair scars on 68% of species and 25% of individual gastropods, and 66% of species and 32% of individuals were drilled.

Deep-sea hydrothermal vents, hydrocarbon cold seeps, and whale falls (e.g., German et al., 2011), found at variable depths, might be expected to show predation patterns that differ from those of other deep-water environments because they are patchy and transient habitats characterized by chemosynthesis. Few predators are specialized to vent environments, and only those opportunistic predators with sulfide tolerance are able to invade from adjacent areas (Voight, 2000). Nevertheless, predation may still be important in structuring vent communities, as indicated by manipulative field experiments (Micheli et al., 2002). The most extreme but also the most productive environments occur closest to the vent; in those environments, predation exerts the greatest influence on community structure as large epibenthic predators (especially zoarcid fish) selectively remove small mobile grazers and facilitate recruitment of sessile invertebrates (Micheli et al., 2002). Evidence of sublethal predation is common at deep-sea vents (Rhoads et al., 1982; Voight, 2000), although some apparent damage may not be the result of predation (Voight, 2000).

Hydrocarbon seep communities may be structured by predation. Modern cold seeps in the Sea of Okhotsk vary faunally along a depth gradient; a dramatic increase in shelled seep megafauna at 250–450 m depth was attributed to a decline in predators such as crabs, asteroids, and carnivorous gastropods (Sahling et al., 2003). Amano et al. (2010) also observed differences in community structure with depth for Miocene seeps in the Japan Sea back-arc basin and suggested that a lack of predatory gastropods at deeper sites was responsible. Eocene-to-Miocene seep deposits in western Washington state, USA, also showed a decline in predator abundance and increase in proportion of obligate seep taxa with depth (Kiel, 2010). Direct evidence of predation at cold seeps is rare, but drill holes have been reported at low frequencies for some sites of Cretaceous age and younger (see Amano and Kiel, 2007; Hryniewicz et al., 2019, and references therein). Durophagous predation in cold seep environments is also known. For example, Kiel et al. (2016) suggested that repair scar frequencies among Oligocene seep bivalve taxa from Japan attributed to crabs were inversely related to sulfide concentrations. Both durophagous crustaceans and fishes were present in ancient cold seeps, particularly from the Mesozoic onwards for the former (e.g., Klompaker et al., 2018). The first evidence of drilling on a whale fall community was reported by Amano and Kiel (2007) from the Miocene of Japan. They stated that drilling frequency for the chemosymbiotic bivalve prey was low (DF = 0.02) in comparison to those reported from shallow-water deposits, likely because the prey may be protected by predation-detering metabolites produced by their symbionts. However, various authors have reported relatively high predation intensities for shallow-water lucinids, which also bear chemosymbionts (Chattopadhyay et al., 2015; Kelley and Hansen,

1993, 2006; Zuschin and Ebner, 2015).

Thus, the relationship between predation and water depth is not straightforward. Many (but not all) studies support a decline in predation with depth and yet, even in extreme habitats with abundant life such as deep-sea hydrothermal vents and cold seeps, predation may play a substantial role in structuring communities. The factors controlling the intensity and nature of predation along depth gradients are complex, as indicated by the contradictory evidence that has been compiled in studies of predation and water depth.

4.2. Different habitats and ecology

In addition to broad-scale patterns of predation with water depth, predation also varies with finer-scale differences in depositional environment. Several aspects of the depositional environment are likely to affect patterns in predation. Oxygen and nutrients (discussed in Sections 4.3 and 4.4) affect most predator-prey systems, whereas substrate is important mainly for benthic ecosystems. Nektonic predators are less affected by substrate, although depositional environment does affect preservation of evidence of such systems in the fossil record (see examples in Delsett et al., 2016; Godwin, 1998; Joyce, 2000; Zatoń and Rakociński, 2014), as it does for benthic predator-prey systems (Selly et al., 2016).

Work with modern systems indicates that the type of substrate affects the distribution of benthic species (Peterson, 1991). For instance, within the Red Sea (Egypt), regular echinoids most often occur on hard substrates and irregular echinoids in soft substrates, within which species distribution is controlled further by sediment grain size (Nebelsick, 1995). Locomotion operates differently for organisms moving within sand, mud, or on top of hard or soft substrates (Vermeij, 2017); thus, life mode varies with substrate. Organisms occupy more permanent burrows in cohesive mud, exhibiting morphologies that ensure stability within the substrate, whereas sand dwellers with streamlined morphologies can burrow actively (Vermeij, 2017). Suspension feeders are more common in sandy substrates and deposit feeders in finer-grained sediments that would clog the feeding apparatuses of suspension feeders (Peterson, 1991; Snelgrove, 1999; see also Nesbitt, 1995, for an Eocene example). Life mode may affect prey vulnerability, although those effects may vary depending on predators. For example, epifauna are more exposed than infauna to predators such as crabs and fish, whereas infauna may be more vulnerable to predation by infaunal predators such as naticid gastropods, as exemplified by greater drilling frequency in Red Sea infaunal prey when comparing to epifaunal prey (Chattopadhyay et al., 2015). In addition, Red Sea deposit feeders were less frequently drilled when compared to suspension feeders and chemoautotrophs (Chattopadhyay et al., 2015), perhaps because they tend to be more mobile. Similarly, Sawyer and Zuschin (2010) found that suspension-feeding mollusks in the northern Adriatic experienced more frequent drilling predation than did other life modes, perhaps because they were both highly abundant and less active.

A major factor affecting substrate type (and consequently life modes of the organisms present) is water energy. In general, predation appears to be less intense in high-energy environments. Water turbulence, caused by high flow speed or coarse sediment, may interfere with chemoreception of prey by predators (Weissburg and Zimmer-Faust, 1993) and with predator locomotion and ability to forage (Robles, 1987). Wilson (1991) noted that sediment type affects the ability of predators to excavate prey from the substrate. For example, feeding experiments indicated that the blue crab *Callinectes sapidus* consumed more hard clams (*Mercenaria mercenaria*) in sand and sand/mud substrates than in shell or gravel substrates that experienced relatively greater water flow velocities (Arnold, 1984).

The effects of differences in water energy are particularly apparent in intertidal areas. Predators such as crabs tend to be smaller and less abundant in higher-energy areas of the intertidal where foraging time is shorter (see Molinaro et al., 2014). Shell repair on the gastropod

Chlorostoma is less frequent in high-energy compared to sheltered intertidal areas of Barkley Sound, British Columbia, Canada, corresponding to the lower intensity of crab predation (i.e., attack frequency) in the high-energy areas (Molinaro et al., 2014). Cadée et al. (1997) observed a wide range of variation in repair frequency within four gastropod species in different intertidal microhabitats of the northern Gulf of California, but a general decrease of repair frequency with increasing environmental energy occurred (see discussion in Molinaro et al., 2014). However, Schmidt (1989) found greater frequencies of gastropod shell repair in rocky than sandy habitats in the northern Gulf of California.

Other stressors are present in intertidal habitats compared to sublittoral environments (Peterson, 1991). At low tide, organisms are subjected to temperature changes and desiccation, although organisms living within the sediment are buffered somewhat from these stresses compared to those in rocky intertidal habitats. Intertidal areas are also susceptible to salinity changes due to input of fresh water. These stresses all increase with elevation on shore, as does exposure to predation from terrestrial organisms such as shorebirds (e.g., Cadée, 1994, 1995). In contrast, organisms found lower on the shoreline are exposed to predators that follow incoming tides to forage in the intertidal (e.g., crabs and rays). Thus, zonation of both prey and predators can be expected both in rocky and soft-sediment intertidal areas.

The intensity of predation also appears to differ between intertidal and sublittoral areas. For instance, Sawyer and Zuschin (2010) found greater drilling predation on mollusk assemblages and lower taxa in the sublittoral northern Adriatic Sea (4–15 m depth) than in the intertidal (27.4% versus 1.4%), and similar results were obtained for the Red Sea (Zuschin and Ebner, 2015). They linked these differences to deleterious effects of subaerial exposure and variation in salinity and temperature on intertidal predators.

Patterns in predation among sublittoral environments are less clear cut. Studies by Chattopadhyay et al. (2015, 2014b), at depths < 52 m in the Red Sea, found no trends in drilling predation on mollusks with depth; fine-grained sediments showed greater DF (0.20) than sandy (0.17) or reef (0.13) substrates, but differences were not statistically significant. Sawyer and Zuschin (2010) found that Adriatic samples from muddy substrates varied more in drilling metrics than did those from sandy bottoms; bivalve families generally had greater DF in muddy than sandy environments but gastropods showed the opposite pattern, although results varied among molluscan families. Among coral reef-associated mollusks of the Gulf of Aqaba (northern Red Sea), bivalves exhibited significantly greater drilling intensity in samples from muddy sand near a patch reef than from gravelly sand near a fringing reef, but gastropod prey showed the opposite pattern of drilling relative to environment (Hausmann et al., 2018). Nebelsick and Kowalewski (1999) found statistically significantly lower DF on echinoids in sand and coral patches in the Red Sea compared to other substrates (muddy sand, sand, sand and seagrass, seagrass, coral carpet); the composition of the echinoid fauna also varied among facies. Drilling frequencies varied widely among sites, even within the same facies, although it was inversely correlated with the abundance of the echinoid species *Fibularia ovulum*. Nebelsick and Kowalewski (1999) hypothesized that the widely varying drilling frequencies were linked to spatial variation in the abundance of predatory cassid gastropods. Predation by cassids in the Caribbean is affected by the presence of reefs (Leviton and Genovese, 1989); mortality of the sea urchin *Diadema* is much greater on sand substrates than in artificial reef or rock environments, suggesting that *Diadema* is commonly associated with reefs because they represent a refuge from their predators.

Seagrass habitats are also thought to provide a refuge from predation for both epifaunal and infaunal prey (Snelgrove, 1999; Wilson, 1991) (see also Section 6.1). Invertebrates occupying areas of dense vegetation are less subject to fish predation (Heck and Thoman, 1981). Seagrass roots bind sediment and are thought to interfere with digging activities of predators; Peterson (1982) found greater densities of the

bivalves *Mercenaria* and *Chione* in vegetated habitats and less mortality from whelk predation than in plots from which seagrass was removed experimentally. Increased species richness in seagrass habitats has also been attributed to inhibition of predation by vegetation (Snelgrove, 1999).

How do these observations of environmental variation of predation in the modern environment translate to the fossil record? Relatively few studies in the fossil record address the relationship of predation to depositional environment. Most such work has focused on variation in drilling predation, and results are not straightforward. Hansen and Kelley (1995) compared drilling predation in six facies of the Eocene Moodys Branch Formation from the US Gulf Coastal Plain, ranging from fine sand deposited in an open bay or lagoon to sandy clay deposited on the outer middle shelf. No consistent pattern was found in successful or failed drilling along the environmental gradient for common prey species or the assemblage as a whole, and DF did not correlate with mean grain size. However, DF correlated with relative abundance of both naticid gastropod drillers and the preferred prey species (i.e., lucinid and corbulid bivalves and turritellid and hipponicid gastropods). Thus, the greatest effect of substrate on predation was in determining the taxonomic composition of the prey faunas, a result similar to that reported by Nebelsick and Kowalewski (1999) for modern Red Sea echinoids. Zlotnik and Ceranka (2005) also suggested that the abundance of cassid gastropod predators may have been responsible for significantly greater drilling on the echinoid *Echinocyamus pusillus* in lower-energy, fine-grained sand compared to coarse-grained sand in the Miocene of Poland, but they were unable to test that hypothesis. No variation in drilling within sublithofacies was found.

Hoffmeister and Kowalewski (2001) found geographically varying patterns in drilling in the Miocene of Europe; Boreal DF on mollusks were greater in sand facies and Paratethys DF were greater in clay facies, indicating that factors other than substrate affect drilling predation (e.g., salinity, temperature). Paratethys localities experienced fluctuations in salinity that would have been most pronounced in nearshore samples where drilling was less frequent. Hoffmeister and Kowalewski (2001) suggested that the chemical processes employed during drilling by naticid and muricid gastropods may have been affected by salinity. In another study of Miocene Paratethyan mollusks, Sawyer and Zuschin (2011) found variation in the frequency of successful and failed drilling between intertidal and sublittoral samples, but whether the differences were significant depended on the taxonomic level of analysis and which stage of the Miocene was examined. Intertidal habitats may have varied more in drilling predation (4–16%) than did sublittoral (4–13%). The drilling intensity in the more near-shore/estuarine conditions of the regional Karpatian Stage tended to be lower than in the more normal marine conditions of the regional Badenian Stage. These results are consistent with observed differences in drilling between modern Adriatic intertidal and sublittoral environments (Sawyer and Zuschin, 2010). Salinity was also posited by Chattopadhyay et al. (2016) as a factor affecting drilling on mollusks in the Eocene of the Paris Basin. Three localities, representing slightly different depositional environments, differed statistically in DF at the assemblage and genus levels. The locality representing the greatest terrestrial input experienced the lowest drilling frequencies (DF = 0.003), whereas localities from the most stable, deeper water, environment recorded the highest drilling frequencies (DF = 0.25). Conversely, a study on modern mollusks from the Bahamas found no relationship between DF and salinity (Selly et al., 2018).

Unvegetated soft substrates appear to have different patterns of predation in the fossil record than reef or seagrass environments. Daley et al. (2007) compared drilling predation on the infaunal bivalve *Chione elevata* between the Pleistocene Bermont and overlying Fort Thompson formations of Florida, USA. The Bermont exhibited a greater DF and less size selectivity of *Chione* prey. Because the seagrass environment of the Bermont impeded burrowing, infaunal bivalves were less abundant and less diverse than in the Fort Thompson. Daley et al. (2007)

concluded that limited prey alternatives in the Bermont led to more intense, less size-selective predation on *Chione* by predatory naticid gastropods. Habitat (seagrass, reef, unvegetated soft sediment) was also considered important in determining differences in predation among families of infaunal bivalves by Leonard-Pingel and Jackson (2013) in the Neogene of Panama and Costa Rica. Genera of venerid bivalves, which mainly occurred in unvegetated sand, were drilled significantly less than lucinid genera, which occupied seagrass habitats. Leonard-Pingel and Jackson (2013) suggested that the small size and shallow depth of burrowing of lucinids made them more vulnerable to drilling predation. They also noted high drilling of cemented epifauna, which are common in reefs. A statistically significant increase in drilling across 11 million years in the Caribbean Neogene was attributed to an increase in coral reef and seagrass environments by Leonard-Pingel and Jackson (2016); genera typically inhabiting these biogenic habitats were drilled two to four times as much as genera characteristic of soft sediments. This change was accompanied by a shift in dominance of drillers from infaunal naticid gastropods (more common in soft sediments) to epifaunal muricids (dominant in the biogenic environments). Thus, conclusions that seagrass and reefs are refuges from predation, as argued for modern environments, does not seem consistent with observations of drilling predation in the fossil record.

The relationship between predation and depositional environment is not straightforward. Most information from the fossil record comes from drilling gastropod predators and their molluscan and echinoid prey. Drilling appears to vary with environment, but different studies have suggested different, often contradictory, relationships between predation intensity and environmental factors. Most studies have concluded that habitat needs to be taken into account when making comparisons across space and time, but general principles are difficult to derive. Interpretations of long-term patterns in predation must recognize that substrates themselves have evolved; increases in bioturbation, evolution of seagrasses, and the activities of organisms that break up hard substrata (e.g., parrotfishes) have modified depositional environments, especially during the Cenozoic (Vermeij, 2017). These changes have created new habitats and new opportunities for both predators and prey.

4.3. Oxygen

The presence of free oxygen is vital to metazoan predation and, indeed, was a limiting factor in animal physiology and body size through geologic time (Payne et al., 2009). The increasing influence of oxygenic photosynthesis on the hydrosphere and atmosphere, beginning during the Great Oxidation Event (2.5 Ga), led to a protracted and stepwise oxygenation of the Earth system (Eriksson et al., 2013; Fike et al., 2006; McFadden et al., 2008) with modern pO₂ being reached by the early Paleozoic (Canfield, 2005). Sperling et al. (2013) highlighted the importance of even small increases of dissolved oxygen in enabling the metabolically intense feeding mode of predation through a meta-analysis of polychaete feeding mode in oxygen minimum zones of the modern ocean. They argued that increasing dissolved oxygen in Ediacaran oceans made evolutionary arms races between predators and prey possible, which played a key role in the Cambrian Explosion. Edwards et al. (2017) linked the Great Ordovician Biodiversification Event to increasing oxygenation. Perhaps not coincidentally, predation intensity seems to have increased concurrently during the Late Ordovician (Huntley and Kowalewski, 2007).

Oxygen, though not analyzed as frequently as other environmental factors, is known to influence predator-prey interactions over shorter time scales and in modern ecosystems. The species richness and density of predatory fish (in this case, tuna and billfish) in the open ocean is strongly related to both sea-surface temperature and dissolved oxygen (Worm et al., 2005). This relationship is likely linked to predator physiology, because tuna cardiac function and depth range are limited by oxygen availability (Worm et al., 2005). Conducting a series of in

situ hypoxia and anoxia experiments in the northern Adriatic Sea, Riedel et al. (2008b) demonstrated that the anemone *Cereus pedunculatus* and the gastropod *Hexaplex trunculus* continued predatory feeding during moderate hypoxia, whereas decapod crustaceans were more susceptible to hypoxia and anoxia as revealed by altered behavior that exposed them to their own predators and elevated mortality (Haselmair et al., 2010; Riedel et al., 2012). In feeding experiments meant to replicate predation of Red Sea bream larvae by jellyfish and juvenile Spanish mackerel, Shoji et al. (2005) offered prey items to predators across a range of sub-lethal low dissolved oxygen conditions. The Spanish mackerel individuals swam slower, displayed a higher gill ventilation rate, and consumed fewer bream larvae with less dissolved oxygen. The jellyfish, however, displayed no change in bell contraction rate and consumed more Red Sea bream larvae under oxygen stress, suggesting that seasonal hypoxia could alter the relative importance of these predators in their natural estuarine habitats in Japan. Breitburg et al. (1994) reported similar results among larval naked goby prey, wherein decreased dissolved oxygen concentrations led to increased predation by the scyphomedusan “sea nettle” and increased physiological stress on and decreased predation by both the adult naked goby and juvenile striped bass from the Chesapeake Bay, eastern USA. In a comprehensive approach integrating live-collected, death assemblage, archaeological, and fossil specimens, Casey et al. (2014) examined community composition and predator-prey interactions along an oxygen stress gradient induced by eutrophication in Long Island Sound, northeastern USA. The authors demonstrated that drilling predation and taxonomic agreement between live-collected and death assemblage samples were greatest in locations most affected by low oxygen levels, contrary to the findings on eutrophication of Kidwell (2013, 2007) and Kidwell and Tomašových (2013). Rather, disturbance by shell fishing outside of the severely hypoxic zone was the primary source of ecological disruption.

Oxygen stress can, of course, also influence the prey side of predator-prey interactions. The experiments of Long et al. (2008) demonstrated that decreased oxygen significantly reduced the burrowing depth of the estuarine infaunal bivalve *Macoma balthica*, presumably increasing its vulnerability to predatory attacks. Likewise, the duration of time that the freshwater to brackish bivalve *Corbicula fluminea* is able to close its shell in a defensive posture following a simulated attack by a predator is significantly reduced under oxygen stress (Saloom and Scot Duncan, 2005). Even though this taxon is known to reduce its metabolic activity by an order of magnitude when its valves are closed and maintain an aerobic metabolism for 5–10 h (Ortmann and Grieshaber, 2003), conditions of reduced dissolved oxygen can make it more susceptible to its predators.

In conclusion, free oxygen has likely played an important, though currently understudied, role in shaping predator-prey interactions through geologic time. At the coarsest of time scales, the oxygenation of the atmosphere and hydrosphere enabled, but did not necessarily guarantee, the dramatic increase in body size, diversity, and increasing complexity of metabolically expensive biotic interactions recorded through the Geozoic (Knoll and Bambach, 2000; Payne et al., 2009; Schiffbauer et al., 2016; Sperling et al., 2013). Over shorter time scales, the lack of oxygen has been shown to influence the behaviors of predators and prey and have unexpected consequences to ecosystem function. It is unclear how fluctuations in oxygen throughout the Phanerozoic have modified predator-prey interactions at a variety of temporal and spatial scales and such will likely be a fruitful avenue for future research.

4.4. Nutrients and food scarcity

The relationship between predation and overall nutrient availability or primary productivity is not always clear, even though productivity has been identified as a factor influencing predator-prey interactions (Bohannan and Lenski, 2000; Holt et al., 1994; Leibold, 1989). Both

theoretical and experimental studies predict a positive correlation between prey population size and rate of prey consumption by predators (Case, 2000; Holling, 1959; Kaunzinger and Morin, 1998; Ricker, 1941). Because prey population size is often strongly influenced by primary productivity, one might expect a positive correlation between productivity and the intensity of predation. However, this hypothesis may not hold true for all marine invertebrates. In a study of the effects of decreasing planktonic productivity in the Caribbean due to the closure of the Central American Seaway (~3.5 Ma), Leonard-Pingel and Jackson (2016) showed a negative relationship between regional productivity and drilling predation intensity, contrary to the theoretical prediction. They inferred that the changes in predation intensity were driven primarily by a change in habitats rather than a decline in productivity.

Increase in nutrients may also affect predation intensity indirectly. Excess nutrient loading (eutrophication) often causes hypoxia, which in turn may change prey-predator interactions (see also above). Hypoxia has been linked to a decreased capacity to drill prey by predatory gastropods (Das and Stickle, 1993; Person et al., 1967). Predatory groups may differ in susceptibility to hypoxia (Levin et al., 2009) and their different responses may lead to a complex pattern of predation in an ecosystem affected by hypoxia (Casey et al., 2014; see also Section 4.3). Because of such complex interplay of variables, the relationship between predation intensity and primary production is still unresolved.

In addition to overall nutrient availability, fluctuating levels of local resources also affect organisms. Heterogeneity in environmental attributes leading to ecological patchiness often results in spatial variation in resources (MacArthur and Pianka, 1966). Consequently, a predator may face intermittent events of saturation and starvation (Menge, 1972). The issue of starvation has not been considered directly in the standard cost-benefit analysis of prey profitability. Such models often fail to predict the pattern of prey choice in resource-limited ecosystems. The standard cost-benefit model, developed from optimal foraging theory, addresses optimal diet and optimal allocation of foraging time to patches independently (Heller, 1980). Such models often fail to predict the pattern of prey choice in resource-limited ecosystems. One way to modify the model is to allow the predator's assessment of prey to vary with levels of hunger. In that case, a predator approaching satiation acts as if prey were abundant and demonstrates highly selective behavior (Charnov, 1976; Pulliam, 1974; Schoener, 1971). However, Richards (1983) demonstrated the opposite effect using a two-prey theoretical model. The model showed that predators expand their prey choice near satiation to include lower-value prey. This means that if a small amount of a high-value prey is required, a predator can be satiated faster if it attacks the first item it encounters rather than searching for a high-value prey. With low patch density, where the encounter rate with high-value prey is low, the model predicts that a specialist would expand its prey choice near satiation. A successful predator following this rule becomes an “expanding specialist,” starting as a specialist and then expanding its diet after some time in the patch (Heller, 1980).

Experimental studies have demonstrated significantly different behavioral traits among starved predators (including lack of selectivity of prey, higher attack, and feeding rate) compared to satiated ones (Beukema, 1968; Ernsting, 1977; Kislalioglu and Gibson, 1976). Other experiments showed a lack of size selectivity by starved predatory gastropods (Barnett, 1979; Palmer, 1980; Perry, 1987; Wood, 1968), fish (Bence and Murdoch, 1986; Ware, 1972), and a glass worm (Pastorok, 1980). Similar studies showed that the escape response of scavenging snails was diminished by hunger (Morton and Chan, 1999; Stenzler and Atema, 1977). However, the observations for starved predators are not always consistent. For example, Perry (1987) documented a significant drop in attack success for starved predatory gastropods, whereas Das et al. (2015) found a higher rate of attack compared to satiated individuals. Unavailability of preferred prey also has been suggested to initiate change in predatory behavior and often

triggered cannibalism in naticid (Chattopadhyay et al., 2014a) and muricid gastropods (Gordillo, 2013b). As starvation is related to prey availability and varies spatially, starvation-induced behavioral change in predation may help explain spatial variation in predation intensity. Prey availability is also thought to change temporally, potentially controlling predatory behavior through time.

4.5. Temperature

Ample evidence suggests that biotic interactions such as predation can be affected by temperature changes in modern marine ecosystems. In turn, whole ecosystems may be influenced. For example, today's Antarctic shelf bottoms are inhabited primarily by ophiuroids, asteroids, echinoids, and gastropods; no shell-breaking predatory crabs are found on the shelf, but they are present on the continental slope (Aronson et al., 2015a, 2015b; Thatje et al., 2005). As seawater temperatures continue to rise, king crabs (Lithodidae) are expected to invade the shelf, along with other shell-breaking invasive crabs (Aronson et al., 2015a, 2015b), most likely resulting in a decreased prey density and diversity (Smith et al., 2017). Predatory decapods were present in Antarctica until the Miocene and Pliocene (Feldmann and Quilty, 1997; Whittle et al., 2014) and may have disappeared since then due to continued cooling (Whittle et al., 2014).

Various examples indicate that entire food chains are altered by increasing temperatures. From a theoretical perspective, an increase in temperature will result in a rise of metabolic rates and thus a higher energetic demand for all species. The latter may not always be met for top predators that have a relatively small population size and are thus more prone to extinction (Kordas et al., 2011). A change in the food chain was shown experimentally for aquatic microbes, as communities in warmer conditions lost proportionally more top predators and herbivores, while autotrophs and bacterivores became more abundant (Petchey et al., 1999). Conversely, experiments on a rocky-intertidal food chain, consisting of a top crab predator, an intermediate drilling gastropod consumer, and a basal mussel prey, showed no negative impact on the crab and mussel with increasing sea temperatures (Miller et al., 2014). However, the intermediate consumer was negatively impacted, showing a reduction in foraging, growth rate, and growth efficiency (Miller et al., 2014).

Most temperature experiments have involved one predator and one prey species from temperate regions. Based on field and lab experiments, rates of predation by a sea star on mussels dropped significantly with a decrease in temperature (Sanford, 1999, 2002). Warming, on the other hand, substantially reduced spaces devoid of predatory sea stars on rocky shores, negatively impacting mussel abundance (Harley, 2011). In another experiment, a gastropod predator and its barnacle prey were subject to changing temperatures (Harvey and Moore, 2017). Tissue production of the prey was reduced in warmer conditions, but feeding rate of the predator decreased rather than increased, despite the presence of abundant prey items (Harvey and Moore, 2017). Feeding rates of predatory crabs on bivalves rose as temperature was increased in various experiments (Barbeau and Scheibling, 1994; Matheson and Gagnon, 2012; Sanchez-Salazar et al., 1987; Wu et al., 2017).

For both muricid and naticid (drilling) gastropods, various studies have demonstrated that feeding rates on mollusks increase with higher temperatures in controlled lab settings (Ansell, 1982a, 1982b; Edwards and Huebner, 1977; Garton and Stickle, 1980; Hanks, 1957; Manzi, 1970; Miller, 2013). Likewise, long-term lab experiments with seasonal temperature variations also showed a positive correlation of feeding rates and temperature for muricids and naticids (Kingsley-Smith et al., 2003; Lord and Whitlatch, 2013), as did long-term field-based experiments with a naticid driller (Edwards and Huebner, 1977). In yet another experimental design, muricid consumption, energy intake, and body tissue production based on a mussel diet was positively correlated to sea surface temperature at various sites within the Gulf of Maine, USA, along a temperature gradient (Matassa and Trussell, 2015).

Abundant molluscan prey were available in these experiments, which may not always be the case in nature. Thus, whether this change in feeding rates has an effect on overall predation intensity in ecosystems remains to be investigated. Some indication may come from latitudinal trends in drilling frequency across a substantial temperature gradient. Although methods differ, various studies on primarily modern ecosystems have indeed shown decreasing drilling frequencies at higher latitudes (Alexander and Dietl, 2001b; Dudley and Vermeij, 1978; Visaggi and Kelley, 2015), but others have found no obvious correlation (Kelley and Hansen, 2007; Martinelli et al., 2013) or even an opposite trend (Hansen and Kelley, 1995; Vermeij et al., 1989).

Despite the rich molluscan fossil record and dramatic changes in Cenozoic temperature, little is known about the effect of temperature on predator-prey interactions in deep time. An exception is a study on Pleistocene mollusk assemblages from Japan (Chiba and Sato, 2016). Studying drill holes in specimens of the most abundant species in a sequence interpreted to represent a cooling interval from ~0.23–0.15 Ma, they found a significant decrease in drilling frequency as warm-water drillers became less common (Fig. 11A). This decrease coincided with a decline of drill holes located on or near the commissure. Our analysis of the data also indicates that predator-prey size ratios decreased (Fig. 11B), suggesting that predators attacked larger prey relative to their own size. This trend is primarily caused by a decrease in drill-hole size, whereas prey size remained relatively stable throughout this interval. Whether these trends are also observed in other species and within whole assemblages remains to be investigated.

Temperature-related trends in predation may be masked by other factors that can be superimposed on latitudinal or temporal variation in temperature. For example, a study focused on Miocene mollusk assemblages sampled across multiple regions of Europe (Hoffmeister and Kowalewski, 2001) documented less intense drilling predation in the warmer Paratethys basin than in the cooler, higher-latitude region of the northern Atlantic (the Boreal Province). The authors suggested that the observed patterns may be due to fluctuating salinity in the Paratethys that may have limited, at least intermittently, marine drilling predators such as naticids. Conversely, subsequent research found that the complex paleogeographic history of the Paratethys, rather than salinity, might explain the low intensity of drilling (Sawyer and Zuschin, 2011).

A recent study highlighted the effect of cooling on predator-prey interactions during the Eocene in Antarctica (Dietl et al., 2018). Unlike their prediction, cannibalistic drilling among naticids did not decrease during the cooling event, but remained stable. The authors suggested that a coinciding decrease in the abundance of shell-breaking predators stimulated cannibalism in this less risky environment.

4.6. Ocean acidification

Ocean acidification (OA) refers to long-term decreases in seawater pH resulting from the uptake of atmospheric CO₂ by the oceans (Doney et al., 2009). This process has received much attention recently, as it has been discovered that current levels of excess CO₂ in the atmosphere have been absorbed by the oceans, resulting in a 0.1 unit drop in surface ocean pH since the Industrial Revolution and a projected further drop of 0.2–0.3 units by 2100 (Hoegh-Guldberg et al., 2014). Although current anthropogenic OA is the focus of most studies, the occurrence of acidification events in the geologic past is well established (D'Hondt et al., 1994; Hönisch et al., 2012; Zachos et al., 2005). Furthermore, these acidification events were likely not benign, and many have been linked to marine mass extinctions (Clarkson et al., 2015; Kiessling and Simpson, 2011; Veron, 2008). The current increase in oceanic CO₂ and the subsequent drop in pH is thus concerning for extant marine organisms and particularly marine calcifiers, due to the susceptibility of calcified shells to dissolution under OA (Hofmann et al., 2010; Kroeker et al., 2013; Orr et al., 2005; Ries et al., 2009). As a result, an outpouring of experimental evidence has tested for the effects of elevated

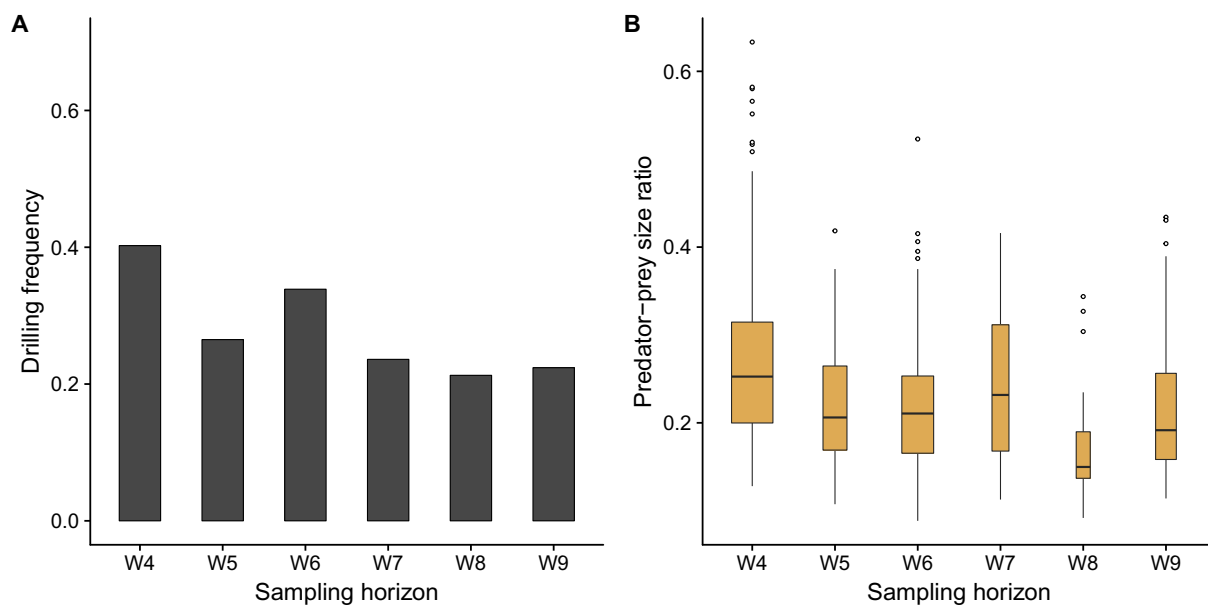


Fig. 11. Decreases in drilling frequencies (A) and predator-prey size ratios (B) during a cooling interval (W4–W9) in the Middle Pleistocene of Japan based on data from Chiba and Sato (2016). The prey used is the bivalve *Glycymeris yessoensis* and the inferred drilling predators are naticid gastropods. Predator-prey size ratios were estimated here by dividing the outer drill-hole diameter by the prey shell length, $n = 748$.

CO₂ on marine organisms, and such evidence may shed light on how acidification events may have affected biotic interactions in the geological past.

Although calcifying marine biota are considered most vulnerable to OA, experimental evidence suggests that species interactions can also be impacted through changes in morphology, physiology, and behavior (see Briffa et al., 2012; Clements and Hunt, 2015; Leduc et al., 2013; Nagelkerken and Munday, 2016, for reviews). For coastal marine mollusks in general, Kroeker et al. (2014) conceptually suggested that energetic and physiological effects of elevated CO₂, along with impacts to chemoreception and behavior, have the capacity to affect predator-prey interactions through altered prey defenses and predator success (Fig. 12). Such impacts have been demonstrated empirically as well. For example, Bibby et al. (2007) reported that OA resulted in thinner shells of the gastropod *Littorina littorea*, which subsequently altered their avoidance behavior of predators (the crab *Carcinus maenas*). Burrowing behavior of infaunal clams is also recognized to be impacted by OA conditions (Clements and Hunt, 2017). Prey defenses in intertidal snails are reportedly affected by OA, rendering snails more susceptible to seastar predation (Jellison et al., 2016). Ocean acidification has also been reported to increase the vulnerability of oysters (*Ostrea lurida*) to drilling predation by invasive oyster drills (*Urosalpinx cinerea*) (Sanford et al., 2014). Wright et al. (2014) also observed increased predation rates of whelks (*Morula marginalba*) feeding on oysters (*Crassostrea gigas*) after 10 days of exposure to OA conditions, although the effect of OA on predation was non-significant after 17 days. Likewise, Amaral et al. (2012) found that oysters (*Saccostrea glomerata*) from more acidic sites were consumed more quickly by whelks (*M. marginalba*) due to their thinner shells. On the other hand, Wu et al. (2017) found that a drop in pH under higher CO₂ conditions resulted in decreased feeding rates of predatory crabs on bivalves. Predator-prey interactions involving a wide variety of mostly fish-eating predatory marine fishes can also be impacted by OA (e.g., Ferrari et al., 2011). Such effects are difficult to establish in the fossil record given the sub-par preservation of predator-prey interactions between fishes. It is thus evident that the nature of biotic interactions across various trophic levels may be affected by acidification, potentially resulting in alterations of entire marine ecosystems (Nagelkerken and Munday, 2016). Furthermore, although multiple-stressor studies remain limited, it is likely that the

combined effects of ocean acidification and other environmental stressors (e.g., temperature) can increase the complexity of such ecological effects (Kroeker et al., 2016; Nagelkerken and Munday, 2016); multi-stressor studies in the context of predator-prey interactions are thus deserving of research attention.

Given the experimental evidence that OA can affect predator-prey relationships, coupled with the notion that biotic interactions can be a

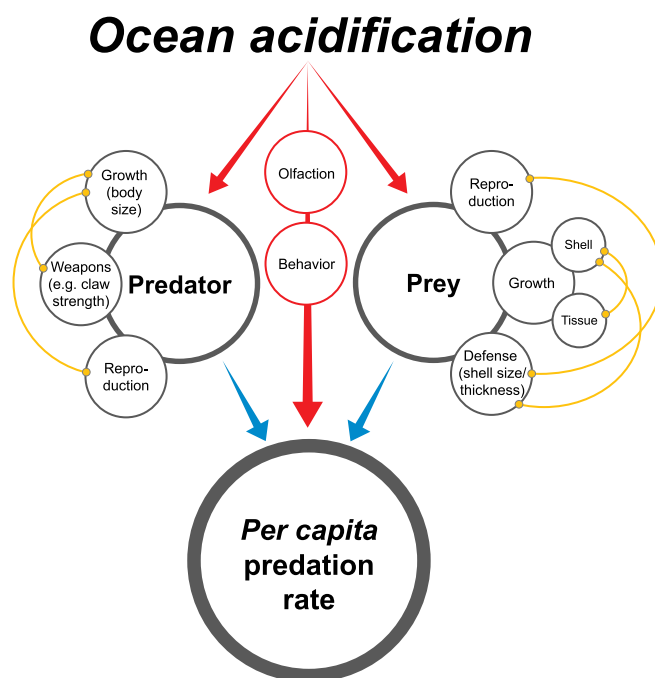


Fig. 12. Conceptual depiction of pathways by which ocean acidification can influence per capita predation rates (modified with permission from Kroeker et al., 2014). Yellow lines linking processes indicate potential trade-offs between growth, reproduction, and defenses (prey) and offenses (predator). Olfactory and behavioral effects apply to both predators and prey. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

function of climate (Blois et al., 2013), the nature of predator-prey interactions throughout geological time may differ between periods of high and low CO₂. Studies have yet to test for effects of acidification events on predator-prey interactions in the fossil record, however. Nonetheless, well-preserved indicators of predator-prey ecology in the fossil record (e.g., drilling predation and repair scars) may shed light on the effect of acidification events on these interactions throughout geological time. Such studies must carefully consider the role of taphonomy, however, given the propensity for increased acidification to weaken shells disproportionately to non-acidification events (e.g., Clements et al., 2018; Waldbusser et al., 2011) and the reported importance of shell dissolution in taphonomy (Cherns et al., 2010; Cherns and Wright, 2000, 2009; Wright et al., 2003). To date, a single study has suggested that OA may have limited effects on shell taphonomy in the context of gastropod drilling predation (Clements et al., 2018); however, much more research is needed regarding the taphonomic role of OA.

5. Behavior of predators

Foraging behaviors by predators have been divided into search, pursuit, and subjugation phases (Griffiths, 1980; Vermeij, 1987; Ziegelmeier, 1954), although these phases are not always easy to separate. Species vary in the proportion of time and energy allocated to each phase of predation. Search and pursuit costs are greater for organisms that forage actively and/or widely, whereas sit-and-wait predators (Pianka, 1974) devote more energy and/or time to subduing their prey (Griffiths, 1980). Hunting mode (sit-and-wait, sit-and-pursue, or active hunting) and habitat domain (the area within the habitat over which foraging occurs) have important consequences for prey behavior, life history, and population demography, which in turn have feedbacks for the predator (Schmitz, 2005). Predator foraging behavior is affected not only by the characteristics and occurrence of the prey, but also by the presence of other predators (Chattopadhyay and Baumiller, 2007, 2010; Hutchings and Herbert, 2013; Lima and Bednekoff, 1999; Trussell et al., 2011).

Only certain types of predator foraging behaviors are evidenced in the fossil record. Evidence of search and pursuit behaviors is rarely preserved and is often circumstantial (Bishop, 1975); paleontological studies of such behaviors mostly have been limited to identifying the behaviors characteristic of particular fossil taxa. Trace fossil evidence includes purported “hunting burrows” (e.g., Babcock, 2003; Bergström, 1973; Brandt et al., 1995; Tarhan et al., 2012) of trilobites. Selly et al. (2016) summarized previous work and criteria for demonstrating trace fossil evidence that trilobites pursued and captured soft-bodied prey; Cambrian (of Missouri, USA) *Rusophycus* trilobite burrows and vermiform burrows intersected at a frequency significantly greater than expected by chance and exhibited evidence of size-selective predatory behavior. At the other end of the size/taxon/temporal spectrum is trace fossil evidence of walrus predation on deep-burrowing bivalves (Gingras et al., 2007). Pleistocene marginal marine sediments of Washington state, USA, contain intersecting bivalve burrows and bowl-shaped excavations interpreted as the result of hydraulic jetting by walruses extracting bivalve prey from the sediment.

More often, inferences about search and pursuit behaviors are based on predator morphologies, especially in reference to extant relatives or analogs. For instance, Massare (1988) used functional morphology to infer swimming speeds and foraging strategies of Mesozoic marine tetrapods. She examined hydrodynamic properties of different body shapes and propulsion styles and calculated that, at the same body size, ichthyosaurs were faster swimmers than plesiosaurs and pliosaurs, which in turn outpaced mosasaurs and crocodiles. She suggested that the long-bodied, slower swimmers were more likely ambush predators, whereas faster swimmers such as ichthyosaurs and pliosaurs were more likely pursuit predators. More recently, Motani (2008) described how physical (e.g., hydrodynamic and optical) principles and comparisons

to modern swimming vertebrates (sharks and tuna) can be incorporated in functional morphological analysis of extinct marine ichthyopterygians. He concluded that parvipelvian ichthyopterygians had advanced cruising abilities and dark-adapted vision that enabled them to forage over a broader area and at greater depth than more basal ichthyopterygians. Foraging involving deep diving has also been inferred from avascular necrosis of bones (indicating the “bends”) in fossil mosasaurs (Martin and Rothschild, 1989; see also Walker and Brett, 2002).

Inferences about the habitat over which a predator searches for prey can also be drawn from prey life mode, at least to a coarse degree. For instance, shell-drilling naticid gastropods usually forage at shallow depths within the substrate (Visaggi et al., 2013), with some exceptions (Grey, 2001; Guerrero and Reymont, 1988; Pahari et al., 2016; Savazzi and Reymont, 1989). However, Dietl (2002) inferred that predators identified as naticids, based on drill-hole shape, hunted and drilled Paleocene pycnodont oysters epifaunally, based on the epifaunal life mode of the prey and the large prey size compared to the predator (as shown by drill-hole size), which would have prevented grappling and transport by the predator.

Evidence of the subjugation (including consumption) phase of predation is preserved more often than evidence of search and pursuit behaviors. Direct evidence of subjugation behaviors occurs in rare cases of exceptional preservation, e.g., an Ordovician asteroid preserved in feeding position on a bivalve, evidencing the early evolution of extraoral feeding by stomach extrusion (Blake and Guensburg, 1994; see also Clarke, 1912, for examples from the Devonian). More often, evidence of subjugation activities is provided by trace fossils; such praedichnia are the focus of most of this paper. Gastric residues, regurgitates, and the like can preserve remains of the victim (Bishop, 1975; see summary for fish predation in McAllister, 2003), sometimes with evidence of the mode of subjugation (Neumann, 2000; Zatoń and Salamon, 2008). Bite marks are often attributed to predation, and their morphology has been linked to possible predators (e.g., Gale et al., 2017, and citations therein; Mapes and Hansen, 1984), although scavenging may be difficult to distinguish from predation (e.g., Collareta et al., 2017a; Hill et al., 2015; Neumann, 2000). Activities such as grazing and crushing produce breakage, which may be accompanied by repair scars when damage is sublethal (see e.g., Nagel-Myers et al., 2009, 2013). Along with breakage and repairs, drill holes yield insight into predator behaviors, including selectivity of prey and prey handling behaviors.

Neontological studies have shown that the degree to which predators are selective of prey differs both among and within taxa as circumstances vary. For instance, predators that are much larger than their prey tend to be less selective (Hawlena and Pérez-Mellado, 2009). Predators tend to be opportunistic if prey are usually scarce (Hughes and Elnor, 1989). Predators exposed to increased risk from their own enemies also are less selective (Hawlena and Pérez-Mellado, 2009; Paul and Herbert, 2014). As discussed further in Section 4.4, even hunger can affect predator selectivity; for instance, Das et al. (2015) demonstrated that hunger decreases prey size selectivity in the naticid gastropod *Natica tigrina*.

In the fossil record, selectivity with respect to prey taxon is usually determined by comparing statistically some measure of predation frequency with the relative abundance of taxa (Kowalewski, 2002; Smith et al., 2018). When predators are non-selective and choose prey randomly, predation should depend on a taxon's relative abundance or accessibility in an assemblage, which in turn should affect how often that prey taxon is encountered by the predator (Martinelli et al., 2015). Using this line of reasoning, Smith et al. (2018) presented a statistical method that tests for selectivity of prey against a null model in which predator preference (as indicated by drilling frequency) for a given prey type is equivalent to that of all other available prey types in the community. Analyses of prey selectivity must take into account the potential effects of time averaging and other taphonomic factors (see Section 3.5). In addition, the relative abundance of species can be altered if

shorter-lived species are disproportionately represented in a fossil assemblage compared to their abundance in life (lifespan bias; Cronin et al., 2018; Kidwell and Rothfus, 2010; Van Valen, 1964; Vermeij and Herbert, 2004) because rapid turnover of generations causes their remains to accumulate faster. Nevertheless, the proportion of specimens of a species exhibiting predation traces should not be affected by lifespan bias. However, apparent selectivity of prey taxa could be affected if different predation tactics were employed on different prey species. For example, if a predator that usually drilled its prey killed a prey item without drilling, as has been reported in some cases (Ansell and Morton, 1987; Kowalewski, 2004; but see Visaggi et al., 2013), no evidence would be left to indicate that the prey item was killed by that predator.

Fossil evidence of breakage and repair has provided some information on taxon selectivity. Although Alexander (1981) concluded that shell-crushing sharks in the upper Mississippian of Utah, USA, were not species-selective of brachiopod prey, other studies have supported selectivity of prey species in the fossil record. For example, the frequency of crinoids with arm regeneration varied significantly among species (0–27%) in the Mississippian of Iowa, USA, with predators targeting the species and individuals with the longest stalks (Gahn and Baumiller, 2005). Paleozoic predators may also have targeted crinoids infested by platyceratid gastropods; Syverson et al. (2018) argued that a correlation between infestation and presence of tegmenal spines in camerate crinoids indicated that spines functioned to deter predation on platyceratids and incidentally on their hosts. Mapes and Chaffin (2003) reported varying percentages (33–83%) of potentially lethal predation breakage among nautiloid genera within the Pennsylvanian Finis Shale of Texas, USA. They concluded that genera with larger-diameter conchs were preferentially selected by predators (probably fish, arthropods, and cephalopods).

Because of problems in interpreting selectivity from repair scars, much of the fossil evidence interpreted as supporting selectivity of prey species comes from shell-drilling predation (but see Leighton, 2002). Examples include prey taxon selectivity of ostracods in the Paleocene of Nigeria (Reyment and Elewa, 2003) and Argentina (Villegas-Martín et al., 2019); mollusks from the Triassic of Italy (Klompmaker et al., 2016a), the Miocene of Bulgaria (Kojumdjieva, 1974) and Poland (Hoffman et al., 1974), and the Pliocene of Spain (Hoffman and Martinell, 1984) and the Netherlands (Klompmaker, 2009); of gastropods in the Miocene of Panama (Fortunato, 2007) and the Pliocene of Ecuador (Walker, 2001); and among brachiopods in the Devonian of New York state, USA (Smith et al., 1985) and the Miocene of Poland (Baumiller and Bitner, 2004). Selectivity of prey taxon is consistent with studies that have found a lack of correlation between drilling frequency and relative abundance (encounter frequency) of taxa (Kelley and Hansen, 2006; Martinelli et al., 2015), although more rigorous tests against null models of predator preference (per Smith et al., 2018) would be welcome. Apparent prey taxon preferences in the fossil record have been linked to various behavioral, ecological, and morphological factors.

Behavioral and ecological factors appear to be important in determining differences in drilling frequencies among fossil taxa (Chattopadhyay and Dutta, 2013; Hoffman et al., 1974). Such factors control the accessibility of prey taxa to predators. For example, Leonard-Pingel and Jackson (2013) found that differential drilling predation on 90 bivalve genera in the Neogene of Panama and Costa Rica was related to their position in the substrate (deep burrowers experienced less predation than shallow burrowers) and mobility (uncemented epifauna were drilled less frequently than cemented bivalves). Sawyer and Zuschin (2010) also noted a high drilling frequency on cementers from level-bottom sands. These results for drilling predators contrast with Harper's (1991) conclusion that cemented bivalves were less vulnerable than byssally-attached species to predation by asteroids and crustaceans that manipulate their prey.

Morphological features of prey may also contribute to patterns of taxon selectivity. Ornamentation has been proposed to explain

differential drilling (and repairs) among taxa (e.g., Battlori and Martinell, 1992; Leighton, 2001; Smith et al., 1985), but results are not straightforward (e.g., Allmon et al., 1990; Kerr and Kelley, 2015; Leighton, 2003b; Leonard-Pingel and Jackson, 2013). Shell microstructure may also play a role in differential drilling, with taxa such as corbulids that contain organic shell layers being less preferred (Kardon, 1998; Kelley, 1988; Lewy and Samtleben, 1979). Ishikawa and Kase (2007) also reported conchiolin layers in 16 species of *Cardiolucina*; the data of Ishikawa and Kase (2007) produce a correlation coefficient $r = -0.4526$ ($p < 0.01$) between DF and the number of conchiolin sheets in the shell, suggesting that predators may avoid (or drill unsuccessfully) taxa with organic sheets. However, Kelley and Hansen (1993, 2006) found corbulids and lucinids (with chemosymbionts, see also Section 4.1) among the preferred prey of naticid drillers across the Cretaceous through Pleistocene of the US Atlantic and Gulf Coastal Plain, attributing their desirability to their sluggish burrowing. In contrast, shell thickness plays an undeniable role in taxon preference of drilling predators (Carriker, 1951; Martinelli et al., 2016). Vermeij (1978) stated that a greatly thickened shell is the only morphological trait known to deter drilling on bivalves.

The importance of shell thickness has been recognized in cost-benefit analyses of prey selectivity by drilling gastropods. Kitchell et al. (1981) argued from experiments and the fossil record (Neogene *Glycymeris* from the US Coastal Plain) that shell-drilling naticid gastropods are optimal foragers that select prey to maximize net energy gain; such predation fits cost-benefit models in which cost is a function of drilling time (i.e., prey shell thickness) and benefit corresponds to biomass (measured as internal volume of the prey shell). Leighton (2001, 2002) argued against the application of optimal foraging theory (Stephens and Krebs, 1986) to predators that encounter prey sequentially (including drillers), but differences in drilling frequencies among taxa appear to fit predictions of cost-benefit analyses in several cases (e.g., Culotta, 1988; Kelley, 1988; Żłotnik and Ceranka, 2005; but see Anderson et al., 1991). Confamilial predation, including cannibalism, by naticids was predictable by cost-benefit analyses (Dietl and Alexander, 1995; Kelley, 1991a). Predictability of cannibalism (see also Brezina et al., 2016) suggests that such behavior is not anomalous, contra Hoffman et al. (1974), Pek and Mikuláš (1996), and Stanton and Nelson (1980).

Prey size is an important component in cost-benefit analyses. Several methods have been used to test for size selectivity (Table 5). A common approach compares size-frequency distributions of attacked and unattacked prey (see discussion in Alexander and Dietl, 2003). In the case of drilling predation, a significant correlation between the size of drilled prey and drill-hole size (corresponding to predator size; Carriker and Gruber, 1999; Hughes and Hughes, 1981; Kitchell et al., 1981; Klompmaker et al., 2017; Kowalewski, 2004) has been interpreted to indicate prey size selectivity (Kitchell, 1986). Numerous authors have reported size selectivity by predators in the fossil record (e.g., Ausich and Gurrola, 1979; Chattopadhyay and Dutta, 2013; Geary et al., 1991; Harper et al., 2018; Hoffman and Martinell, 1984; Kabat and Kohn, 1986; Kelley, 1988; Kitchell, 1986; Klompmaker et al., 2015; Mallick et al., 2013, 2014; Martinell et al., 2012; Nagel-Myers et al., 2013; Pek and Mikuláš, 1996; Żłotnik and Ceranka, 2005). Such size selectivity may be the result of active predator choice, as predicted by optimal foraging theory, but it may also represent mechanical limits to predation (Brown and Haight, 1992). Rodrigues et al. (1987) argued that foot size of naticid gastropods influences prey size choice; naticids can assess prey size using their foot and reject items that exceed the manipulation size limits of the predator (see also Chiba and Sato, 2012; Kabat, 1990; Kitchell et al., 1981; Pahari et al., 2016). This point is supported by reports of greater size selectivity by naticid than muricid gastropod predators (Casey et al., 2015; Kojumdjieva, 1974); naticids wrap their prey in the foot and muricids do not (Carriker and Yochelson, 1968).

Some bivalved prey experienced preferential attacks on a particular valve, which may be related to valve accessibility and/or predator

Table 5

Methods used to test for size selectivity by predators, with a (non-exhaustive) list of studies exemplifying each method.

| Method | Example studies |
|--|--|
| Compare size frequency distributions of attacked and non-attacked prey | Kabat and Kohn (1986) – drilling and repair scars on naticid gastropods, Allmon et al. (1990) – drilling on turritelline gastropods, Geary et al. (1991) – stomatopod holes in gastropods, Hoffmeister and Kowalewski (2001) – drilling on mollusks, Martinell et al. (2012) – drilling on serpulids, Grun et al. (2014) – drilling on echinoids, Chattopadhyay and Dutta (2013) – drilling on bivalves, Mallick et al. (2013, 2014) – drilling on gastropods, Selly et al. (2016) – burrow size of attacked and non-attacked trilobite prey, Takeda et al. (2016) – durophagous predation on ammonoids |
| Compare size frequency distributions of attacked prey and total prey population | Kelley (1982) – drilling on mollusks |
| Compare size distributions for death assemblage and size at attack based on repair scars | Harper et al. (2009) – durophagous predation on brachiopods, Pruden et al. (2018) – durophagous predation on brachiopods |
| Compare predation frequencies for different size classes of prey | Złotnik and Ceranka (2005) – drilling on echinoids, Chattopadhyay et al. (2016) – drilling on mollusks |
| Compare mean and/or median size of attacked and unattacked specimens | Baumiller et al. (2006) – drilling on brachiopods, Daley et al. (2007) – drilling on bivalves, Brezina et al. (2016) – drilling on naticid gastropods |
| Correlate prey size and predator size proxy (e.g., drill hole size, break length) | Kelley (1982) – drilling on mollusks, Hoffman and Martinell (1984) – drilling on mollusks, Kabat and Kohn (1986) – drilling on naticid gastropods, Kelley (1988) – drilling on bivalves, Allmon et al. (1990) – drilling on turritelline gastropods, Hoffmeister and Kowalewski (2001) – drilling on mollusks, Złotnik and Ceranka (2005) – drilling on echinoids, Daley et al. (2007) – drilling on bivalves, Martinell et al. (2012) – drilling on serpulids, Chattopadhyay and Dutta (2013) – drilling on bivalves, Mallick et al. (2013, 2014) – drilling on gastropods, Klompmaker et al. (2015) – drilling on barnacles, Kong et al. (2015) – drilling on bivalves, Meadows et al. (2015) – drilling on echinoids, Chiba and Sato (2016) – drilling on bivalves, Brezina et al. (2016) – drilling on naticid gastropods, Grun et al. (2014, 2017) – drilling on echinoids, Takeda et al. (2016) – durophagous predation on ammonoids |

handling behaviors. Valve preference has been reported for inequivalved bivalve species. For example, predators prefer drilling the right valve in many species of corbulids (De Cauwer, 1985), which may relate to handling behavior of the predator (Anderson, 1992) or the larger size of the right valve (Taylor et al., 1983; Złotnik, 2001). Species that attach to the substrate by one valve, such as oysters, may also experience valve-selective predation (Chattopadhyay and Dutta, 2013, for the Miocene of India; Taylor, 1970, for the Eocene of the Paris Basin).

Handling behaviors may also affect the site on a prey shell that is attacked. Not all predation is site selective (Adegoke and Tevesz, 1974; Battlori and Martinell, 1992; Kabat and Kohn, 1986). Among drilling gastropods, muricids manipulate their prey less and show more random distributions of drill-hole sites on the prey shell compared to naticids (Carriker and Yochelson, 1968; Casey et al., 2015; Stump, 1975; but see Klompmaker et al., 2015, for muricid drilling on barnacles). However, stereotyped drill-hole positions have been reported on a wide range of prey: bivalves (Kelley, 1988; Kong et al., 2017; Taylor, 1970), gastropods (Berg and Nishenko, 1975; Blustein and Anderson, 2016; Taylor, 1970), scaphopods (Klompmaker, 2011; Yochelson et al., 1983), brachiopods (Ausich and Gurrola, 1979; Harper and Wharton, 2000; Smith et al., 1985), echinoids (Kowalewski and Nebelsick, 2003), barnacles (Donovan and Novak, 2015; Klompmaker et al., 2015), ostracods (Villegas-Martín et al., 2019), serpulid polychaetes (Martinell et al., 2012), and foraminifers (Malumián et al., 2007).

Ease of penetration of hard parts also may influence site of attack on the prey shell. Kitchell (1986) recognized that thickness varies across a prey's shell and proposed that predators situate drill holes on thinner areas of the shell. Allmon et al. (1990) stated that gastropods drilled the thinnest part of the shell of turritelline gastropods. Grun et al. (2017) and Meadows et al. (2015) argued that cassid gastropods preferentially attacked the highly porous, more penetrable central aboral area of now fossilized echinoid tests. Other authors have linked drill-hole site to the position of soft parts (Arua and Hoque, 1989; Klompmaker, 2011; Smith et al., 1985; Yochelson et al., 1983), including muscles (Chattopadhyay and Dutta, 2013; Leighton, 2001). Todd and Harper (2011) suggested that stereotyped drill-hole position in the bivalve *Venericor* from the Eocene of England was due to octopods injecting toxins into the

posterior adductor muscle. Alexander and Dietl (2001a, 2003) attributed the position of repair scars on bivalve shells to prey anatomy, with attacks focused on areas where soft tissues are exposed, as well as to predator behavior (i.e., posterior repairs resulted from siphon nipping, whereas ventral repairs resulted from shell wedging and chipping or occurred on species with ventral egress of the foot). For gastropod prey, stereotypy of drill-hole site may also reflect handling behaviors that block egress of the prey's foot, thus preventing escape (Berg and Nishenko, 1975; Dietl and Alexander, 2000).

Sometimes the position of attack can be linked to the direction from which predators approached their prey. For example, the position of bite marks on a Pliocene dolphin suggests an attack by a shark from the posterior and subsequently on the dorsal fin (Bianucci et al., 2010; Fig. 13). Although the sample size is small, bite marks on the skulls of Eocene juvenile basilosaurid whales are interpreted to have been made by larger confamilials that attacked primarily from a left lateral position (Fahlke, 2012). Klompmaker et al. (2009) recognized a preference for ventral bite marks near the end of the body chamber, close to the phragmocone, on Mesozoic ammonoids. They concluded that the predators, likely coleoid cephalopods and fish, attacked the ammonoids from behind. Takeda et al. (2016) reached similar conclusions for ventral attacks near the rear of the body chamber of Cretaceous scaphitid ammonoids. Posterior attacks may also have been the norm for predation on trilobites. Babcock (2003) reported that 75% of sublethal predation scars on trilobites occurred on the posterior end and 69% were restricted to the right side of the body. He attributed this lateral preference to the predation tactics suggested by Nedin (1999) for anomalocarids: the predator held one edge of the trilobite in its mouth and flexed the prey back and forth until its exoskeleton broke. Among brachiopods, some studies have found a preference for attacks on the valve closest to the substrate (e.g., Ausich and Gurrola, 1979; Leighton, 2001; Rohr, 1976), which may be consistent with an infaunal predator attacking from beneath the shell.

Handling behavior by a given predator may vary with the type of prey attacked. For instance, octopods drill holes in large prey to inject toxins, but they may not drill smaller prey (Harper, 2006). Similarly, edge-drilling was more frequently used for large bivalve prey of the gastropod *Muricanthus fulvescens*, whereas shell grinding was used often

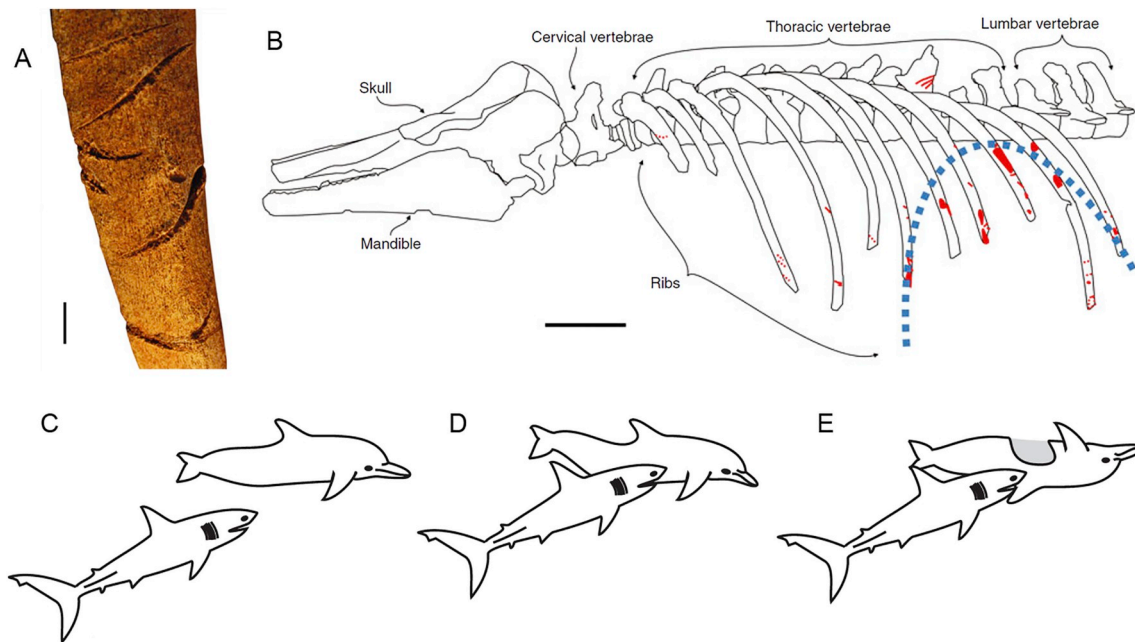


Fig. 13. Inferred shark attack on a dolphin during the Pliocene in Italy. (A) Bite marks on one of the ribs on the right side; scale bar is 50 mm tall. (B) Line drawing of the left side of the dolphin indicating bite marks in red and the location of the possible first main bite with a blue dashed line; scale bar is 100 mm wide. (C–E) Possible sequence of attack by the shark. Modified from [Bianucci et al. \(2010: figs 3–5\)](#). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

for small prey ([Herbert et al., 2016](#)). The muricid gastropod *Hexaplex trunculus* employs both chipping and drilling modes of predation, with large *Hexaplex* preferring to attack mussels by chipping ([Sawyer et al., 2009](#)). [Gordillo and Archuby \(2012\)](#) found that the gastropod *Acanthina monodon* used different attack techniques (drilling vs. wedging valves apart) on different species of mussels in Tierra del Fuego, Argentina. Muricid gastropods may employ drilling of prey or kleptoparasitism, in which they “steal” the food from other muricids by feeding through the gape of a bivalve or displacing another muricid from the hole it drilled; [Ishida \(2005\)](#) found muricid species differed in the degree to which they used each technique depending on factors such as proboscis morphology, penetration cost, and ingestion speed. In the fossil record, drilling is likely to be more preservable than alternative techniques, which may lead to underestimation of mortality. Shell-drilling gastropods may employ wall drilling or edge drilling to attack bivalves ([Chattopadhyay et al., 2014b](#); [Dietl et al., 2004](#)). In the case of muricids, edge drilling has been linked to the competitiveness of the environment because drilling at the shell margin (where the valve is thinner) is quicker than wall drilling, but the muricid risks amputation of its drilling apparatus by closure of the valves of the prey ([Burrell, 1975](#); [Herbert, 2018](#)). Behavioral changes in wall drilling vs edge drilling are readily traceable in the fossil record ([Dietl et al., 2004](#)).

Prey handling behaviors also determine whether feeding is solitary or aggregative. Because they use the foot to envelop individual prey items, naticid gastropods typically forage singly (although group scavenging has been observed; JCC, pers. obs.). In contrast, group foraging is possible for gastropods that do not wrap the foot around victims. The muricid gastropod *Stramonita haemastoma* (oyster drill) frequently exhibits group foraging in the field ([Brown and Alexander, 1994](#)). In the laboratory, snails were more likely to join an ongoing attack, especially on a large oyster, than initiate an attack on a different prey. Most snails attempted to drill their prey, suggesting that multiple drill holes in single prey items in the fossil record could represent aggregative feeding by muricids. [Złotnik and Ceranka \(2005\)](#) concluded that, in the Miocene of Poland, small cassid gastropods often attacked echinoids through group attacks, as occurs in the Recent ([Hughes and Hughes, 1971](#)). However, larger cassids, which cover their prey more

entirely with the foot ([Hughes and Hughes, 1981](#)), were only able to attack singly, based on evidence from drill holes ([Złotnik and Ceranka, 2005](#)). Multiple drill holes on an echinoid specimen varied slightly in size but were all small and widely spaced, indicating that more than one small cassid, spaced across the echinoid test, was responsible for the drilling. However, large holes drilled by large cassids were almost always found singly. Thus, ontogenetic changes in behavior occurred, which concurs with studies reporting ontogenetic behavioral changes in various Recent drilling gastropods ([Berg, 1976](#); [Clements and Rawlings, 2014](#); [Gosselin and Chia, 1996](#); [Urrutia and Navarro, 2001](#)). In the fossil record, [Złotnik \(2001\)](#) also documented ontogenetic changes in naticid behavior in the Miocene of Poland; small naticid drill holes on *Corbula gibba* were less stereotyped in position and more occurred on the left valve, compared to larger drill holes. Likewise, [Klompaker \(2012\)](#) reported that Pliocene serpulids from the Netherlands were primarily drilled by small naticids, suggesting an ontogenetic change in diet.

[Kelley \(1988\)](#) found that, among Miocene bivalves of Maryland, USA, prey species that displayed the most stereotyped drill-hole positions and greatest prey size selectivity also exhibited higher percentages of successful drill holes. If stereotyped behavior leads to greater success by the predator, it might be expected that stereotypy would increase through deep time. Some evidence exists to support this hypothesis. Shell-drilling naticid and muricid gastropods diversified during the Cretaceous. [Taylor et al. \(1983\)](#) reported a lack of size selectivity of mollusk prey of drilling gastropods in the Albian Blackdown Greensand of England, early in this diversification. [Reyment et al. \(1987\)](#) found that drill-hole size was not correlated with ostracod prey size in the Late Cretaceous (Santonian) of Israel but was strongly correlated in the Paleocene of Nigeria. Also, drill-hole site stereotypy may have been less pronounced during the Cretaceous ([Berg, 1978](#); [Kitchell, 1986](#); but see [Kelley and Hansen, 1993, 1996](#)). In addition, cost-benefit analyses of prey selectivity based on the model of [Kitchell et al. \(1981\)](#) were more consistent with drilling frequencies for Neogene than Paleogene assemblages ([Kelley and Hansen, 1996, 2003](#)). [Hagadorn and Boyajian \(1997\)](#) found that size selectivity by drilling gastropods on US Coastal Plain specimens of *Turritella*, as indicated by correlations of drill-hole diameter and prey size, increased between the Miocene and Pliocene.

However, Paul and Herbert (2014) found decreasing size stereotypy of naticid and muricid predation on Neogene *Chione* bivalves of Florida, USA, as did Dietl and Alexander (2000) for Miocene to Recent confamilial predation on naticids of the mid-Atlantic Coastal Plain, USA.

Some authors have reported an increase in efficiency of predators through time. Babcock (2003) interpreted a decrease in frequency of sublethal scars on trilobites after the Cambrian as indicative of attacks by more efficient predators. Dietl (2003a) found that stereotypy of attack site by shell-chipping *Sinistrofulgur* gastropods on the bivalve *Mercenaria* increased from the Pliocene to Pleistocene of Florida. The increased proportion of attacks at the ventral shell margin of *Mercenaria* was accompanied by a decrease in failed attacks and interpreted as an improvement in the gastropod's predatory efficiency. *Sinistrofulgur* may break its own shell while attempting to chip open prey; truncate-embayed scars occur when the predator prematurely resumes feeding without adequately repairing such breaks (Dietl, 2003a). A Plio-Pleistocene decline in the frequency of truncate-embayed scars on the predator's shell was interpreted as evolutionary change in predator behavior to limit such premature feeding (Dietl, 2003a). For drilling predation, prey effectiveness (proportion of drill holes that are incomplete, i.e., unsuccessful) was assessed for Cretaceous - Quaternary gastropod and bivalve samples from the US Coastal Plain. Although fluctuations occurred among samples, Kelley et al. (2001) found a significant decrease in failed drilling, consistent with an increase in predator efficiency after the Paleogene.

Other reported temporal trends in predatory behavior involve a shift in the position of attack on the prey. For instance, Dietl and Alexander (2000) found that the drill-hole site shifted to a position closer to the umbilicus in confamilial predation of naticid gastropods from the Miocene to Recent; this position would have prevented egress of the prey's foot. Hagadorn and Boyajian (1997) found that the preferred site for drilling on *Turritella* shifted away from the aperture in the Miocene to Pliocene of the US Coastal Plain, and Mondal et al. (2017) reported that confamilial drill holes in naticids became more randomly positioned after the Oligocene. In many cases a shift in attack site may involve a change of predator, rather than an evolutionary change in behavior within a lineage of predator. Thomas (1976) found that drill-hole positions on bivalves of the *Glycymeris americana* lineage shifted from the umbo in the Miocene to a central position in the Plio-Pleistocene of the US Coastal Plain, which he hypothesized represented either a shift in predatory behavior or predator species. Amano (2006) likewise observed a shift in the drill-hole position on *Glycymeris* from Japan between the Miocene and Pleistocene, but different predators were involved. Similar conclusions were reached by Chiba and Sato (2016) for *Glycymeris* in the Pleistocene of Japan; changes in drill-hole site and predator-prey size relationships were linked to the abundance of warm- and cool-climate naticid species. Babcock (2003) noted a shift in position of repair scars on trilobites after the Cambrian, with an increase in the percent of scars on the left side or occurring on both sides of trilobites. He linked these changes to a change in predators, from anomalocarids to the adaptive radiation of cephalopods and fish.

6. Antipredatory features and other defense strategies in deep time

Extant and ancient marine organisms use a variety of active defensive behavioral strategies, such as hiding and active movements once caught (e.g., Harper and Skelton, 1993a; Kohn, 1999), and passive defense strategies, including camouflage, toxicity, shell structure, thickness, and ornamentation. Several authors have summarized the literature about defensive traits and behavior of shelled prey (Brett and Walker, 2002; Harper and Kelley, 2012; Harper and Skelton, 1993a; Kohn, 1999; Vermeij, 1987, 1995; Walker and Brett, 2002; Zuschin et al., 2003), drawing heavily from modern observations. Therefore, we review the types of defenses with a strong focus on studies that include fossils or have implications for the fossil record. Notably, the

development of defensive traits, such as the type of coiling and the degree of ornamentation, in response to increased predation intensity is one of the cornerstones of the Mesozoic Marine Revolution and its mid-Paleozoic precursor during which predation intensity is thought to have increased (Signor and Brett, 1984; Vermeij, 1977).

6.1. Active defenses

Active defense strategies (see also Vermeij, 1987) by modern marine prey include mobility (e.g., Baumiller and Messing, 2007), immobilization of predators with byssal threads (e.g., Day et al., 1991; Petraitis, 1987), deep burrowing (e.g., Fregeau, 1991; Visaggi et al., 2013; Walker and Brett, 2002), hiding on the sea bottom (e.g., Klompmaker and Fraaije, 2012), enrollment (e.g., Babcock, 2003), wounding the feeding apparatus of predators (e.g., Burrell, 1975), active movements to dislodge the predator or avoid being caught (e.g., Edwards, 1969; Laws and Laws, 1972; Pratt, 1974), and autotomy (Baumiller et al., 2008; Oji and Okamoto, 1994). Of those, only mobility, burrowing/hiding, and enrollment may be evaluated in detail for the fossil record.

Prey that are more mobile have a greater chance of escaping predators. Although the absolute speed of prey is difficult to determine from marine body fossils or trackways, whether animals were able to move at all is easier to infer for some fossil taxa. Over the Mesozoic, Gorzelak et al. (2012) found that genus richness of sessile crinoids is negatively correlated with that of predatory sea urchins, whereas a positive correlation was suggested between motile crinoids and predatory sea urchins. They argued that crinoid motility is an effective escape strategy, which is consistent with evidence of crawling by extant and fossil stalked crinoids and the crawling and swimming abilities of comatulid crinoids (Baumiller and Messing, 2007; Brom et al., 2018; Meyer and Macurda, 1977; Neto de Carvalho et al., 2016). A similar conclusion was reached for post-Paleozoic crinoids: the appearance and evolutionary success of motile crinoids starting in the Triassic was suggested to be related to the radiation of echinoid predators with more advanced feeding apparatuses (Baumiller et al., 2010a) or the rise of bony fishes (Meyer and Macurda, 1977). Conversely, motility was not found to be an important factor explaining drilling frequency for modern bivalves in the Red Sea (Chattopadhyay et al., 2015). On very long time scales, Bambach et al. (2002) documented a proportional increase of motile marine metazoan genera throughout the Phanerozoic, from ~20% in the Cambrian to ~80% in the late Cenozoic.

Some marine organisms may have evolved burrowing behavior to gain access to food within the sediment. However, for some taxa, including filter-feeding siphonate bivalves, the ability to burrow may represent an escape strategy from predators. Burrowing is effective against various predators because crustaceans, fishes, and epifaunal drilling predators have more difficulty in detecting and accessing buried prey. An example from the fossil record (Miocene of the Netherlands) illustrates the effect of depth: Van Schooten (1998) inferred that specimens of the bivalve *Pelecypora polytropa nysti* up to 7 cm in size were drilled by (infaunal) naticid gastropods only in the upper half of the shell in their buried life position. Further evidence is provided by Neogene bivalves from Panama: infaunal bivalves, especially deep burrowers, exhibit relatively low drilling frequencies (Leonard-Pingel and Jackson, 2013, but see Chattopadhyay et al., 2015, for extant bivalves from the Red Sea). Over the course of the Phanerozoic, the proportion of genera interpreted to live infaunally increased from ~5% in the early Cambrian to ~20% in the Cenozoic, with a major rise starting in the Mesozoic (Bush and Bambach, 2011). Burrowing depth has also increased throughout the Phanerozoic (Ausich and Bottjer, 1982; Bottjer and Ausich, 1986; Thayer, 1983).

Enrollment, often interpreted as a defense mechanism against predators or adverse environmental conditions, is found primarily in fossil arthropods such as trilobites (Clarkson and Henry, 1973; Esteve et al., 2011; Ortega-Hernandez et al., 2013), horseshoe crabs (Anderson and

Selden, 1997), and isopods (Fraaije et al., 2019). Other enrolled specimens include annelid-like animals from the Cambrian (e.g., Chen and Zhou, 1997; Yang et al., 2014). The best-studied temporal patterns in enrollment (or conglobation) are for trilobites; the percentage of enrolled specimens increased throughout the Paleozoic as trilobite enrollment became more efficient due to skeletal modifications (Esteve et al., 2011, 2017). Differentiating environmentally and predatory-induced enrollment appears difficult, but most enrollments may be environmentally induced by sedimentation events that buried the enrolled specimens, because an attack typically does not bury the prey specimens (see also Brett et al., 2012).

Preventative defense may occur when organisms seek shelter within shells, bore into hard substrates, or live in cryptic habitats. Hermit crabs, which have taken up residency in gastropod and ammonite shells, represent a prime example of such behavior (e.g., Fraaije, 2003; Jagt et al., 2006). Many examples of specimens found in shells are known from the fossil record, including trilobites in Paleozoic brachiopods, hyoliths, nautiloids, and trilobites (Brett, 1977; Davis et al., 2001; Fatka et al., 2009; Fatka and Budil, 2014; Zong et al., 2016); echinoids, bivalves, heteromorph ammonites, and ophiuroids in Mesozoic ammonites (Ernst, 1967; Hagdorn, 1998; Matsumoto and Nihongi, 1979); decapods in Triassic–Miocene cephalopods, echinoids, and bivalves (Fraaije and Pennings, 2006; Fraaye and Jäger, 1995a; Gašparič et al., 2015; Klompmaker and Fraaije, 2012; Landman et al., 2014; Schulz, 2002) (Fig. 14); and fishes in Jurassic–Cretaceous ammonites and inoceramid bivalves (Fraaye and Jäger, 1995b; Nyborg et al., 2014; Stewart, 1990; Vullo et al., 2009), among others. Refuge from predators, including long-term residency (=inquilism), is a potential reason for the co-occurrences, but it is difficult to exclude other possibilities, such as scavenging upon the decaying soft tissue inside the host's shell; a place to reproduce, die, or molt for arthropods; post-mortem transport into the shell; or even accidental trapping due to shelter closure (e.g., Campbell et al., 1997). The preservation style, motility of the animal inside the shell, relative abundance of the animal outside the shell, sedimentary environment, the frequency of co-occurrence, and modern observations can help to infer the most likely reason for co-occurrence.

Other organisms construct their own domiciles in a variety of hard substrates by embedment or boring (e.g., Tapanila, 2005; Taylor and Wilson, 2003), and, consequently, are fairly well protected against predators. Organisms that create such domiciles include some sponges (e.g., Bromley, 1970; Bromley et al., 1984), bivalves (e.g., Savazzi, 1999), decapods (e.g., Klompmaker et al., 2016b), annelids (e.g., Ishikawa and Kase, 2007; Voigt, 1975), and bryozoans (e.g., Pohowsky, 1978).

Various cryptic habitats provide opportunities to hide from predators. Submarine caves are known from the fossil record, particularly in the Jurassic (Reolid and Molina, 2010; Taylor and Palmer, 1994; Wilson, 1998). Reefs (Kiessling, 2009; Wood, 1999) and seagrasses (e.g., Ivany et al., 1990; Moissette et al., 2007; Reich et al., 2015) are other habitats with an ancient origin in which organisms are likely to seek shelter from predators.

6.2. Passive defenses

Passive defenses are common among shelled organisms and include sculptural features such as ornamentation, thick shells, large size, cementation, certain shell microstructures, shell curvature and shape, size and shape of the aperture, tight shell closure, mimicry of more difficult or dangerous prey (Kohn, 1999), clumping (Casey and Chattopadhyay, 2008; Okamura, 1986), and toxicity/unpalatability (e.g., Thayer, 1985; Thayer and Allmon, 1990; Tyler et al., 2013). In contrast to more active methods of defense, most of the passive defense strategies have been studied to some extent in the fossil record (except for mimicry, clumping, and toxicity/unpalatability, which are not discussed further here).

Shell sculpture includes spines, ribs, nodes, varices, corrugations, and buttresses. The effectiveness against predation varies among features and with the type and strength of the predator. Paleontological studies have evaluated the effectiveness of ornamentation in deterring predators for some prey and time intervals. For example, moderate ribs of Cenozoic bivalves were most effective against drilling predation by naticid gastropods (Klompmaker and Kelley, 2015). Late Cretaceous ribbed oysters have a higher repair scar frequency from unsuccessful attacks by shell-breaking predators than unornamented ones (Dietl et al., 2000), and drill holes were less common in ornamented gastropods from the Eocene (Arua and Hoque, 1987). For cephalopods, Jurassic ammonites that are smooth have more incised injuries than ornamented ones (Kröger, 2002), whereas more ornamented Jurassic and Cretaceous ammonites showed fewer repair scars (Kerr and Kelley, 2015). Brachiopods with lamellae were less frequently drilled than smooth congeners in the Devonian (Leighton, 2003b) and drill holes in a Devonian brachiopod with spines had a lower success rate than those in a morphologically similar taxon without spines (Leighton, 2001). Finally, for arthropods, Santonian and Paleocene ornamented ostracods were suggested to have a lower drilling percentage than smooth ones (Reyment et al., 1987, but see Villegas-Martín et al., 2019) and enlarged thoracic spines in Cambrian trilobites may have served as a protection against durophagous predators (Pates and Bicknell, 2019).

Although the effectiveness of ornamentation against several types of predation has been demonstrated in deep time, few studies have addressed whether ornamentation evolved in response to predators (evolutionary adaptation), whether it was co-opted (exaptation sensu Gould and Vrba, 1982), or whether it is due to phenotypic plasticity/inducible defense (e.g., Appleton and Palmer, 1988; Sherker et al., 2017). For example, exaptation to drilling was inferred for ribs in astartid bivalves because ribs appeared within the lineage before drilling became common (Klompmaker and Kelley, 2015). The same reasoning was applied to spines in some bivalves (Stone, 1998) and ribs in Jurassic–Cretaceous nautiloids (Bardhan and Halder, 2000). Conversely, ribbing was suggested to be adaptive within lineages of gryphaeid oysters (Dietl et al., 2000).

Various paleontological studies have suggested an increase in ornamentation through geological time for gastropods (Alexander and Dietl, 2003; Dietl and Alexander, 1998; Vermeij, 1987), ammonites (Ward, 1981, but see Kerr and Kelley, 2015), nautiloids (Bardhan and Halder, 2000), brachiopods (Alexander, 1990), some crinoids (Syverson et al., 2018), and Paleozoic invertebrates in general (Signor and Brett, 1984). Often, predation pressure has been hypothesized to be the causal mechanism for such trends, but much testing remains to be done on other groups, on different time intervals, and within specific lineages. An important caveat is that shell sculpture may not necessarily be defensive but serve other functions. For example, Tyler et al. (2014) demonstrated in laboratory experiments that limpet prey with stronger sculpture experienced higher mortality from crabs and suggested that enhanced sculpture primarily served to mitigate against thermal stress, and not as anti-predatory defense. Another study suggested that large spines on the epifaunal bivalve *Spondylus* promote epibiont coverage and not necessarily deter predators (Carlson Jones, 2003). Thus, it is important that we do not automatically assume that all ribs, spines, and other ornamental structures perform an anti-predator function. Fossil prey taxa should be tested on a case-by-case basis without making any a priori assumptions about the role of ornamentation.

Shell thickness is positively correlated with shell strength, and thicker shells are more difficult and/or time-consuming to break or drill (Alexander, 1990; Carriker, 1951; Kelley and Hansen, 2003; Kitchell et al., 1981; Kohn, 1999; Zuschin et al., 2003). Thus, an increase in shell thickness is one of the most effective ways to deter predators. Drilling is indeed more likely for thinner shells for infaunal reef bivalves (Martinelli et al., 2016). Several studies have suggested an active role for predation in shell thickening. A Plio-Pleistocene increase in thickness of a single species of bivalve in Florida was suggested to be in

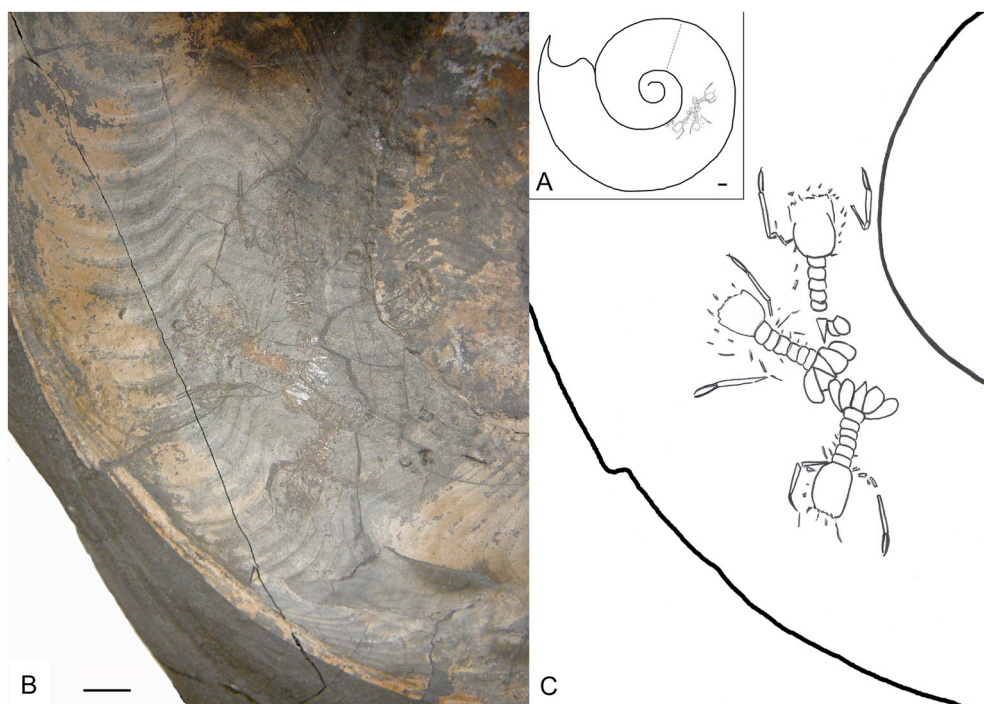


Fig. 14. A compressed specimen of the Early Jurassic (Toarcian) ammonite *Harpoceras falciferum* from Germany with only the translucent periostracum preserved shows three erylid lobsters within the body chamber. (A) Drawing of entire ammonite specimen with the position of lobsters. (B, C) Photo and drawing of part of the body chamber containing the three lobsters. Scale bar widths: 10 mm. Modified from Klompmaker and Fraaije (2012: figs 3B, 4).

response to predators and/or warmer temperature (Roopnarine and Beussink, 1999). In more detailed studies, Miocene bivalves that suffered the highest drilling frequencies experienced the largest increase in shell thickness over the course of 3 million years, leading to a reduction in drilling (Kelley, 1989, 1991b). Similarly, shell thickness increases in other Neogene bivalves were accompanied by an increase in incomplete drilling (Kent cited by Vermeij, 1987, p. 311). Furthermore, some bivalve prey increased in thickness during the Eocene-Oligocene, while naticid drillers did not respond with offensive adaptations (Kelley and Hansen, 2001). Longer-term trends in shell thickness through time are difficult to obtain due to diagenetic processes dissolving all or part of the shell layers (Harper and Skelton, 1993a).

As specimens grow, shell thickness typically increases, but specimens also may reach a size beyond which they become too difficult to manipulate by a given-sized predator (a size refugium, also termed size refuge or escape size; see Kelley, 1991b; Leighton, 2002) (Fig. 15). Size refugia have been demonstrated in the fossil record, as shown for repair scars in Late Ordovician and Devonian brachiopods (Alexander, 1986a; Johnsen et al., 2013; Richards and Leighton, 2012), drill holes in Devonian brachiopods (Sheehan and Lesperance, 1978), repair scars in Middle Ordovician endocerid cephalopods (Kröger, 2011), drill holes in Neogene bivalves (Grey et al., 2006; Leonard-Pingel and Jackson, 2013), and drill holes in Cretaceous and Cenozoic turritellid gastropods (Allmon et al., 1990; Mallick et al., 2013). Another type of proposed size refuge is an increase in the proportion of failed drilling attempts for larger size classes, which was documented for Eocene brachiopods (Schimmel et al., 2012) and Pliocene gastropods (Martinell et al., 2010). However, this lower success rate does not necessarily imply increased safety from predators, because successful predation intensity for large specimens may still be comparable to or greater than that for smaller size classes when larger specimens are attacked more frequently (see for example Schimmel et al., 2012). Additionally, a prey that has reached a size refuge from one type of predator may become more attractive to a different predator.

Cementation of bivalves has been shown experimentally to be effective against predation by crabs and starfish, as it inhibits manipulation (Harper, 1991). The same paper suggested a causal link between the rise of cementing bivalves and increased predation pressure in the Mesozoic. Conversely, cementation is not effective against drilling by

epifaunal drillers that do not manipulate their prey (such as Muricidae), as shown by the higher drilling frequencies in modern and Neogene cementing bivalves (Leonard-Pingel and Jackson, 2013; Sawyer and Zuschin, 2010). Another group of cementing organisms, barnacles, is also drilled primarily by muricids in the Cretaceous–Cenozoic, albeit at assemblage-level percentages of < 10% (Klompmaker et al., 2015). Cementation also occurred among fossil brachiopods and annelids (Alexander, 2001; Walker and Brett, 2002), but the extent to which it was effective against predation is unknown.

Shell microstructure greatly influences shell strength against predation (Alexander and Dietl, 2003; Zuschin et al., 2003, and references). Of all microstructural types, a nacreous microstructure with an organic matrix appears to be the strongest structure and one of the oldest (Furuhashi et al., 2009; Vendrasco et al., 2010; Zuschin et al., 2003). Indeed, organic content enhances shell strength, but the metabolic cost to produce organics can be 20 times greater than for calcium carbonate (Palmer, 1992). Several examples show the importance of

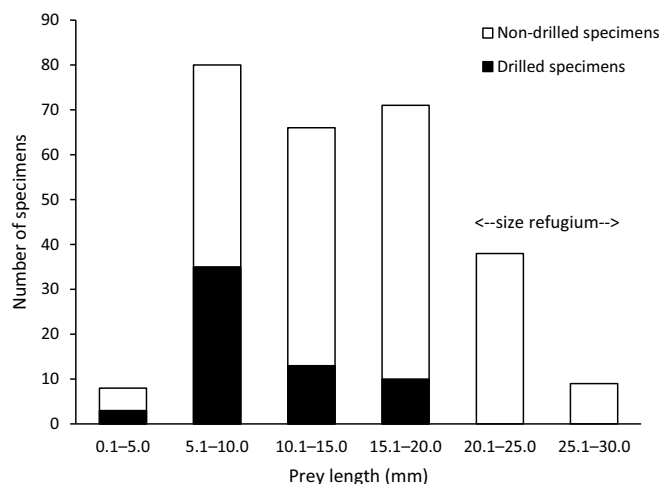


Fig. 15. Example of a size refugium against drilling predation reached at 20 mm shell length by the late Maastrichtian gastropod *Bellifusus* aff. *indicus* from India. Data from Mallick et al. (2014).

organic material in deterring predation. Epifaunal mussels with a thick periostracum are less prone to drilling by muricids than are mussels from which this organic layer was removed (Harper and Skelton, 1993b), but whether the periostracum evolved as an adaptation to drilling remains unclear as periostraca do not preserve well in the fossil record. So-called conchiolin (organic) sheets or layers, present within some bivalves, are effective against drilling in modern and fossil corbulids (De Cauwer, 1985; Harper, 1994; Kardon, 1998; Kelley, 1988; Klompmaker, 2009; Lewy and Samtleben, 1979) and fossil lucinids (Ishikawa and Kase, 2007). Such layers are also thought to inhibit crack propagation (Kardon, 1998). Whether conchiolin layers are an adaptation (Harper, 1994), an exaptation (Ishikawa and Kase, 2007; Kardon, 1998), serve a function other than anti-predatory (Anderson, 1992; Anderson et al., 1991), or are an artifact of construction (Walker and Brett, 2002) requires further testing.

Shell curvature and general shape affect predation success (e.g., Alexander and Dietl, 2003; Kohn, 1999; Vermeij, 1978; Zuschin et al., 2003). Examples of anti-predatory functions are known from the fossil record: biconvex brachiopods show lower repair scar frequencies than concavo-convex shells (Alexander, 1986a; Forcino et al., 2017); Jurassic ammonites with rounded whorls are suggested to be less susceptible to predatory attacks (Kröger, 2002); and open and planispiral coiling and the presence of umbilica in gastropods decreased through time, trends that were linked to increased predation (e.g., Signor and Brett, 1984; Vermeij, 1987).

Various strategies are used to protect the shell openings of coiled taxa such as gastropods and cephalopods. Apertures have narrowed through time for gastropods (Vermeij, 1987). For serpenticonic ammonites, common in the Mesozoic (Parent et al., 2010), small apertures relative to the total body size provided better protection against apertural attacks than relatively large apertures (Kröger, 2002). Some gastropods developed an operculum that closes the aperture (e.g., Bandel, 2008; Kaim and Sztajner, 2005; Norton, 1988) (Fig. 16). Opercula or opercula-like structures apparently evolved independently at least thirteen times in gastropods (Vermeij and Williams, 2007) and are known from the Early Ordovician onward (Yochelson, 1979). Gastropod opercula are effective against predators; 40% of gastropods with an operculum that were ingested whole by fishes survived the digestive tract (Norton, 1988). Opercular thickness of turbinid gastropods is greater in the tropics, where predation pressure is thought to be higher (Vermeij and Williams, 2007). Opercula are also known from Cambrian Mobergellidae (Topper and Skovsted, 2017) and fossil nautiloids (e.g., Dziki, 1981; Edgecombe and Chatterton, 1987). Considerable debate has arisen about the function of ammonite aptychi and anaptychi (summarized in Parent et al., 2014). Although aptychi are considered to have functioned mainly as lower jaws, many workers have suggested an anti-predatory function as well (e.g., Keupp et al., 2016; Lehmann and Kulicki, 1990; Parent et al., 2014; Seilacher, 1993; Tanabe et al., 2015).

Tight closure of bivalved animals (ostracods, bivalves, and brachiopods) is one of the main defense mechanisms to avoid leakage of chemical cues that may attract predators, to remain intact when ingested, and to avoid breakage of the shell margin (Vermeij, 1983, 1987). A globose shell, as seen in some bivalves and brachiopods, helps prevent shell breakage at the commissure (Vermeij, 1983). Vermeij (1987: table 11.3) showed that the incidence of crenulated and overlapping valve margins of bivalves increased throughout the Phanerozoic, and crenulated margins occur more frequently in the more dangerous tropics. Alexander (1986a) hypothesized that a commissural ridge in some Ordovician brachiopods evolved in response to predation. Counterintuitively, the proportion of bivalves with vulnerable gaping margins has increased through time, but most such bivalves burrow deeply and, thus, are well protected from most predators (Alexander and Dietl, 2003; Vermeij, 1987).

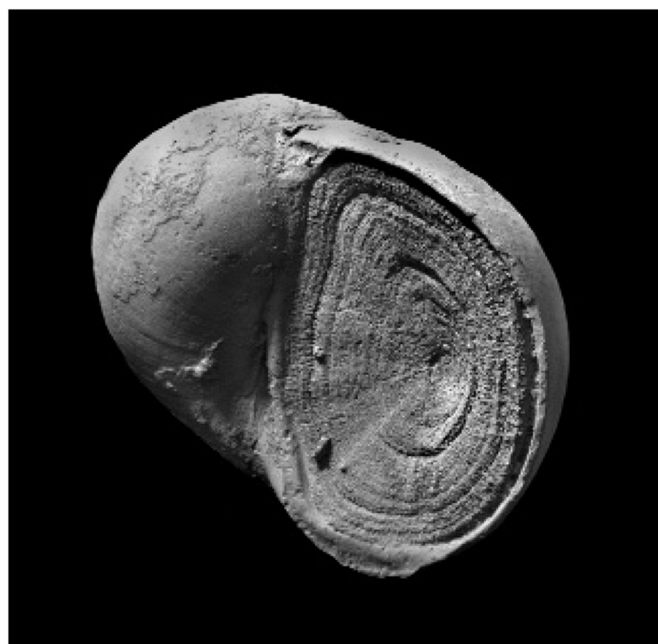


Fig. 16. An operculum still in situ in the Late Triassic gastropod *Fedaiella neritacea* from Italy. Shell height ~22 mm. From Bandel (2008: pl. 1.12).

7. Conclusions and future directions

Research on predation in the marine fossil record started around the mid-19th century, but the topic did not receive much attention until the 1960s, after which a substantial increase in literature is recorded that continues to date. Studies that have contributed to this field include neontological experiments, ecological observations, and paleontological analyses of predation. In addition to documenting some predation traces from less commonly studied prey types, localities, and geologic periods, recent studies also focused on testing hypotheses or validating specific predictions of evolutionary paleoecology. The fossil record of predation in ancient marine ecosystems is dominated by trace fossils, particularly drill holes and, to a lesser extent, repair scars. Mollusks are the clade most often studied as prey and inferred predators, with most data thus far deriving from the Cenozoic of Europe and North America. More work is needed on types of predation other than drilling and shell crushing, taxa other than mollusks, and evidence of predation from understudied regions and pre-Cretaceous times. Additionally, documentation of whole assemblages for which predation intensity appears low is important to better assess temporal trends in predation intensity.

Any analysis of predator-prey interactions requires proper recognition of these interactions. Correcting for abiotic damage is necessary to calculate predatory breakage intensity more accurately; we propose 12 criteria for distinguishing between biotic and abiotic shell damage. We further identify 16 criteria to differentiate predatory from parasitic traces, particularly for drill holes. When a predatory event has been confirmed, the identity of the predator can be pursued. We find that studies focused on gut contents and predatory attacks preserved in place identify predators to the genus- or species-levels more frequently than is the case for other indicators of predation. Taphonomic and other factors can distort the recognition of patterns of predation and should be evaluated cautiously before drawing conclusions about the occurrence and intensity of predator-prey interactions. Many such factors can be identified and accounted for by following specific protocols, but more research is needed.

More work is also required to develop general principles for understanding how predation varies among environments. Factors that affect predation, including taxonomic composition of communities, prey life modes, and predator foraging strategies, vary with water depth

and depositional environment, but patterns are not straightforward. Studies of predation in the marine fossil record must take habitat into account. Oxygen, temperature, and ocean acidification are known to affect predator-prey interactions in modern marine ecosystems, but their role in shaping predator-prey interactions through geologic time is currently understudied. The relationship between predation intensity and primary production in today's oceans is still unresolved.

The behavior of predators and prey defense have been studied more thoroughly. The marine fossil record preserves evidence of subjugation, and to a lesser extent search and pursuit, behaviors of predators, including prey selectivity and handling behaviors. Changes in prey behavioral stereotypy and efficiency have occurred through time. Two broad categories of prey defense, active and passive defenses, have been studied in the fossil record with varying levels of detail. These defenses include mobility, burrowing/hiding, enrollment, ornamentation, shell thickness, size, cementation, shell microstructure, shell curvature and shape, size and shape of the aperture, and shell closure. Future research could investigate whether these defenses evolved in response to predation (adaptation) or whether they developed for a different purpose but were subsequently co-opted to serve as anti-predatory features (exaptation).

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References

- Adegoke, O.S., Tevesz, M.J.S., 1974. Gastropod predation patterns in the Eocene of Nigeria. *Lethaia* 7, 17–24. <https://doi.org/10.1111/j.1502-3931.1974.tb00881.x>.
- Alexander, R.R., 1975. Phenotypic lability of the brachiopod *Rafinesquina alternata* (Ordovician) and its correlation with the sedimentologic regime. *J. Paleontol.* 49, 607–618.
- Alexander, R.R., 1981. Predation scars preserved in Chesterian brachiopods: probable culprits and evolutionary consequences for the articulates. *J. Paleontol.* 55, 192–203.
- Alexander, R.R., 1984. Comparative hydrodynamic stability of brachiopod shells on current-scoured arenaceous substrates. *Lethaia* 17, 17–32. <https://doi.org/10.1111/j.1502-3931.1984.tb00662.x>.
- Alexander, R.R., 1986a. Resistance to and repair of shell breakage induced by durophages in Late Ordovician brachiopods. *J. Paleontol.* 60, 273–285. <https://doi.org/10.1017/S0022336000021806>.
- Alexander, R.R., 1986b. Life orientation and post-mortem reorientation of Chesterian brachiopod shells by paleocurrents. *PALAIOS* 1, 303–311. <https://doi.org/10.2307/3514693>.
- Alexander, R.R., 1990. Mechanical strength of shells of selected extant articulate brachiopods: Implications for Paleozoic morphologic trends. *Hist. Biol.* 3, 169–188. <https://doi.org/10.1080/08912969009386520>.
- Alexander, R.R., 2001. Functional morphology and biomechanics of articulate brachiopod shells. In: Carlson, S.J., Sandy, M.R. (Eds.), *Brachiopods Ancient and Modern. A Tribute to G. Arthur Cooper*, The Paleontological Society Papers, pp. 145–170.
- Alexander, R.R., Dietl, G.P., 2001a. Shell repair frequencies in New Jersey bivalves: a recent baseline for tests of escalation with Tertiary, Mid-Atlantic congeners. *PALAIOS* 16, 354–371. [https://doi.org/10.1669/0883-1351\(2001\)016<0354:SRFINJ>2.0.CO;2](https://doi.org/10.1669/0883-1351(2001)016<0354:SRFINJ>2.0.CO;2).
- Alexander, R.R., Dietl, G.P., 2001b. Latitudinal trends in naticid predation on *Anadara ovalis* (Bruguiere, 1789) and *Divalinga quadriscutata* (Orbigny, 1842) from New Jersey to the Florida Keys. *Am. Malacol. Bull.* 16, 179–194.
- Alexander, R.R., Dietl, G.P., 2003. The fossil record of shell-breaking predation on marine bivalves and gastropods. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 141–176. https://doi.org/10.1007/978-1-4615-0161-9_7.
- Alexander, R.R., Dietl, G.P., 2005. Non-predatory shell damage in Neogene Western Atlantic deep-burrowing bivalves. *PALAIOS* 20, 280–295. <https://doi.org/10.2110/palo.2004.p04-29>.
- Allen, J.R.L., 1984. Experiments on the settling, overturning and entrainment of bivalve shells and related models. *Sedimentology* 31, 227–250. <https://doi.org/10.1111/j.1365-3091.1984.tb01961.x>.
- Allmon, W.D., Nieh, J.C., Norris, R.D., 1990. Drilling and peeling of turrilline gastropods since the Late Cretaceous. *Palaeontology* 33, 595–611.
- Alpert, S.P., Moore, J.N., 1975. Lower Cambrian trace fossil evidence for predation on trilobites. *Lethaia* 8, 223–230. <https://doi.org/10.1111/j.1502-3931.1975.tb00926.x>.
- Alroy, J., Marshall, C.R., Bambach, R.K., Bezusko, K., Foote, M., Fursich, F.T., Hansen, T.A., Holland, S.M., Ivany, L.C., Jablonski, D., Jacobs, D.K., Jones, D.C., Kosnik, M.A., Lidgard, S., Low, S., Miller, A.I., Novack-Gottshall, P.M., Olszewski, T.D., Patzkowsky, M.E., Raup, D.M., Roy, K., Sepkoski, J.J., Sommers, M.G., Wagner, P.J., Webber, A., 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proc. Natl. Acad. Sci.* 98, 6261–6266. <https://doi.org/10.1073/pnas.111144698>.
- Amalfitano, L.C., Dalla Vecchia, F.M., Giusberti, L., Fornaciari, E., Luciani, V., Roghi, G., 2017. Direct evidence of trophic interaction between a large lamniform shark, *Cretodus* sp., and a marine turtle from the Cretaceous of northeastern Italy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 469, 104–121. <https://doi.org/10.1016/j.palaeo.2016.12.044>.
- Amano, K., 2006. Temporal pattern of naticid predation on *Glycymeris yessoensis* (Sowerby) during the late Cenozoic in Japan. *PALAIOS* 21, 369–375. <https://doi.org/10.2110/palo.2005.P05-37e>.
- Amano, K., Kiel, S., 2007. Drill holes in bathymodioline mussels from a Miocene whale-fall community in Hokkaido, Japan. *The Veliger* 49, 265–269.
- Amano, K., Jenkins, R.G., Aikawa, M., Nobuhara, T., 2010. A Miocene chemosynthetic community from the Ogaya Formation in Joetsu: evidence for depth-related ecologic control among fossil seep communities in the Japan Sea back-arc basin. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 286, 164–170. <https://doi.org/10.1016/j.palaeo.2009.12.013>.
- Amaral, V., Cabral, H.N., Bishop, M.J., 2012. Effects of estuarine acidification on predator-prey interactions. *Mar. Ecol. Prog. Ser.* 445, 117–127. <https://doi.org/10.3354/meps09487>.
- Anderson, L.C., 1992. Naticid gastropod predation on corbulid bivalves: Effects of physical factors, morphological features, and statistical artifacts. *PALAIOS* 7, 602–620. <https://doi.org/10.2307/3514872>.
- Anderson, L.L., Selden, P.A., 1997. Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. *Lethaia* 30, 19–31. <https://doi.org/10.1111/j.1502-3931.1997.tb00440.x>.
- Anderson, L.C., Geary, D.H., Nehm, R.H., Allmon, W.D., 1991. A comparative study of naticid gastropod predation on *Varicorbula caloosae* and *Chione cancellata*, Pliocene of Florida, U.S.A. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 85, 29–46. [https://doi.org/10.1016/0031-0182\(91\)90024-L](https://doi.org/10.1016/0031-0182(91)90024-L).
- Anderson, R.C., Wood, J.B., Mather, J.A., 2008. *Octopus vulgaris* in the Caribbean is a specializing generalist. *Mar. Ecol. Prog. Ser.* 371, 199–202. <https://doi.org/10.3354/meps07649>.
- Andrew, C., Howe, P., Paul, C.R.C., Donovan, S.K., 2010. Fatally bitten ammonites from the lower Lias Group (Lower Jurassic) of Lyme Regis, Dorset. *Proc. Yorks. Geol. Soc.* 58, 81–94. <https://doi.org/10.1144/pygs.58.1.276>.
- Andrew, C., Howe, P., Paul, C., 2015. Fatally bitten ammonites from septarian concretions of the 'Marston Marble' (Lower Jurassic, Sinemurian), Somerset, UK, and their taphonomy. *Proc. Geol. Assoc.* 126, 119–129. <https://doi.org/10.1016/j.pgeola.2014.10.006>.
- Ansell, A.D., 1982a. Experimental studies of a benthic predator-prey relationship. I. Feeding, growth, and egg-collar production in long-term cultures of the gastropod drill *Polinices alderi* (Forbes) feeding on the bivalve *Tellina tenuis* (da Costa). *J. Exp. Mar. Biol. Ecol.* 56, 235–255.
- Ansell, A.D., 1982b. Experimental studies of a benthic predator-prey relationship: III. Factors affecting rate of predation and growth in juveniles of the gastropod drill *Polinices catena* (da Costa) in laboratory cultures. *Malacologia* 22, 367–375.
- Ansell, A.D., 1982c. Experimental studies of a benthic predator-prey relationship. II. Energetics of growth and reproduction, and food-conversion efficiencies, in long-term cultures of the gastropod drill *Polinices alderi* (Forbes) feeding on the bivalve *Tellina tenuis* da Costa. *J. Exp. Mar. Biol. Ecol.* 61, 1–29. [https://doi.org/10.1016/0022-0981\(82\)90019-3](https://doi.org/10.1016/0022-0981(82)90019-3).
- Ansell, A.D., Morton, B., 1987. Alternative predation tactics of a tropical naticid gastropod. *J. Exp. Mar. Biol. Ecol.* 111, 109–119. [https://doi.org/10.1016/0022-0981\(87\)90049-9](https://doi.org/10.1016/0022-0981(87)90049-9).
- Appleton, R.D., Palmer, A.R., 1988. Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in a marine gastropod. *Proc. Natl. Acad. Sci.* 85, 4387–4391. <https://doi.org/10.1073/pnas.85.12.4387>.
- Aranki, J.M., 1987. Marine lower Pliocene Ostracoda of southern Spain with notes on recent fauna. *Publ. Palaeontol. Inst. Univ. Upps.* 13, 1–134.
- Arnold, W.S., 1984. The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam, *Mercenaria mercenaria* (Linné). *J. Exp. Mar. Biol. Ecol.* 80, 207–219. [https://doi.org/10.1016/0022-0981\(84\)90150-3](https://doi.org/10.1016/0022-0981(84)90150-3).
- Arnold, J.M., Arnold, K.O., 1969. Some aspects of hole-boring predation by *Octopus vulgaris*. *Am. Zool.* 9, 991–996. <https://doi.org/10.1093/icb/9.3.991>.
- Aronson, R.B., 1987. Predation on fossil and Recent ophiuroids. *Paleobiology* 13, 187–192. <https://doi.org/10.1017/S0094837300008733>.
- Aronson, R.B., 1989. Brittleness beds: Low-predation anachronisms in the British Isles. *Ecology* 70, 856–865. <https://doi.org/10.2307/1941354>.
- Aronson, R.B., 1991. Predation, physical disturbance, and sublethal arm damage in ophiuroids: a Jurassic-Recent comparison. *Mar. Ecol. Prog. Ser.* 74, 91–97.
- Aronson, R.B., 1992. Biology of a scale-independent predator-prey interaction. *Mar. Ecol. Prog. Ser.* 89, 1–13.
- Aronson, R.B., Blake, D.B., 2001. Global climate change and the origin of modern benthic

- communities in Antarctica. *Am. Zool.* 41, 27–39. <https://doi.org/10.1093/icb/41.1.27>.
- Aronson, R.B., Blake, D.B., Oji, T., 1997. Retrograde community structure in the late Eocene of Antarctica. *Geology* 25, 903–906. [https://doi.org/10.1130/0091-7613\(1997\)025<0903:RCSFTL>2.3.CO;2](https://doi.org/10.1130/0091-7613(1997)025<0903:RCSFTL>2.3.CO;2).
- Aronson, R.B., Frederich, M., Price, R., Thatje, S., 2015a. Prospects for the return of shell-crushing crabs to Antarctica. *J. Biogeogr.* 42, 1–7. <https://doi.org/10.1111/jbi.12414>.
- Aronson, R.B., Smith, K.E., Vos, S.C., McClintock, J.B., Amsler, M.O., Moksnes, P.-O., Ellis, D.S., Kaeli, J., Singh, H., Bailey, J.W., Schiferl, J.C., van Woeseik, R., Martin, M.A., Steffel, B.V., Deal, M.E., Lazarus, S.M., Havenhand, J.N., Swalethor, R., Kjellerup, S., Thatje, S., 2015b. No barrier to emergence of bathyal king crabs on the Antarctic shelf. *Proc. Natl. Acad. Sci.* 112, 12997–13002. <https://doi.org/10.1073/pnas.1513962112>.
- Arsenault, M., 1982. *Eusthenopteron foordi*, a predator on *Homalacanthus concinnus* from the Escuminac Formation, Miguasha, Quebec. *Can. J. Earth Sci.* 19, 2214–2217. <https://doi.org/10.1139/e82-195>.
- Arúa, I., Hoque, M., 1987. Predation intensity in an Eocene molluscan assemblage from southeastern Nigeria. *Geol. en Mijnb.* 66, 293–296.
- Arúa, I., Hoque, M., 1989. Predatory gastropod boreholes in an Eocene molluscan assemblage from Nigeria. *Lethaia* 22, 49–59. <https://doi.org/10.1111/j.1502-3931.1989.tb01167.x>.
- Atema, J., Burd, G.D., 1975. A field study of chemotactic responses of the marine mud snail, *Nassarius obsoletus*. *J. Chem. Ecol.* 1, 243–251. <https://doi.org/10.1007/BF00987873>.
- Ausich, W.I., Bottjer, D.J., 1982. Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. *Science* 216, 173–174. <https://doi.org/10.1126/science.216.4542.173>.
- Ausich, W.I., Gurrola, R.A., 1979. Two boring organisms in a lower Mississippian community of southern Indiana. *J. Paleontol.* 53, 335–344.
- Babcock, L.E., 1993. Trilobite malformations and the fossil record of behavioral asymmetry. *J. Paleontol.* 67, 217–229. <https://doi.org/10.1017/S0022336000032145>.
- Babcock, L.E., 2003. Trilobites in Paleozoic predator-prey systems, and their role in reorganization of early Paleozoic ecosystems. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 55–92. https://doi.org/10.1007/978-1-4615-0161-9_4.
- Babcock, L.E., Feldmann, R.M., Wilson, M.T., 1987. Teratology and pathology of some Paleozoic conulariids. *Lethaia* 20, 93–105. <https://doi.org/10.1111/j.1502-3931.1987.tb02025.x>.
- Bańuk, W., Radwański, A., 1996. Stomatopod predation upon gastropods from the Korytnica Basin, and from other classical Miocene localities in Europe. *Acta Geol. Pol.* 46, 279–304.
- Bambach, R.K., Knoll, A.H., Sepkoski, J.J., 2002. Anatomical and ecological constraints on Phanerozoic animal diversity in the marine realm. *Proc. Natl. Acad. Sci.* 99, 6854–6859. <https://doi.org/10.1073/pnas.092150999>.
- Bandel, K., 2008. Operculum shape and construction of some fossil Neritimorpha (Gastropoda) compared to those of modern species of the subclass Vita Malacol. 7, 19–36.
- Barbeau, M.A., Scheibling, R.E., 1994. Temperature effects on predation of juvenile sea scallops [*Placopecten magellanicus* (Gmelin)] by sea stars (*Asterias vulgaris* Verrill) and crabs (*Cancer irroratus* Say). *J. Exp. Mar. Biol. Ecol.* 182, 27–47. [https://doi.org/10.1016/0022-0981\(94\)90209-7](https://doi.org/10.1016/0022-0981(94)90209-7).
- Barco, A., Schiaparelli, S., Houart, R., Oliverio, M., 2012. Cenozoic evolution of Muricidae (Mollusca, Neogastropoda) in the Southern Ocean, with the description of a new subfamily: Pagodulinae, new muricid subfamily. *Zool. Scr.* 41, 596–616. <https://doi.org/10.1111/j.1463-6409.2012.00554.x>.
- Bardack, D., 1965. Anatomy and evolution of chirocentrid fishes. *Univ. Kans. Paleontol. Contrib.* 10, 1–86.
- Bardhan, S., Halder, K., 2000. Sudden origin of ribbing in Jurassic *Paracnoceras* (Nautiloidea) and its bearing on the evolution of ribbing in post-Triassic nautiloids. *Hist. Biol.* 14, 153–168. <https://doi.org/10.1080/10292380009380564>.
- Barnett, B.E., 1979. A laboratory study of predation by the dog-whelk *Nucella lapillus* on the barnacles *Elminius modestus* and *Balanus balanoides*. *J. Mar. Biol. Assoc. U. K.* 59, 299–306. <https://doi.org/10.1017/S0025315400042600>.
- Batllori, J., Martinell, J., 1992. Actividad predatora en moluscos del Mioceno del Penedès (Catalunya). *Rev. Esp. Paleontol.* 7, 24–30.
- Baumiller, T.K., 1990. Non-predatory drilling of Mississippian crinoids by platyceratid gastropods. *Palaeontol.* 33, 743–748.
- Baumiller, T.K., 1993. Boreholes in Devonian blastoids and their implications for boring by platyceratids. *Lethaia* 26, 41–47. <https://doi.org/10.1111/j.1502-3931.1993.tb01508.x>.
- Baumiller, T.K., 1996. Boreholes in the Middle Devonian blastoid *Heteroschisma* and their implications for gastropod drilling. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 123, 343–351. [https://doi.org/10.1016/0031-0182\(95\)00124-7](https://doi.org/10.1016/0031-0182(95)00124-7).
- Baumiller, T.K., 2002. Multi-snail infestation of Devonian crinoids and the nature of platyceratid-crinoid interactions. *Acta Palaeontol. Pol.* 47, 133–139.
- Baumiller, T.K., 2003a. Experimental and biostratigraphic disarticulation of crinoids: taphonomic implications. In: Féral, J.-P., David, B. (Eds.), *Echinoderm Research 2001*. A.A. Balkema Publishers, Lisse, pp. 243–248.
- Baumiller, T.K., 2003b. Evaluating the interaction between platyceratid gastropods and crinoids: a cost-benefit approach. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 201, 199–209. [https://doi.org/10.1016/S0031-0182\(03\)00625-4](https://doi.org/10.1016/S0031-0182(03)00625-4).
- Baumiller, T.K., Bitner, M.A., 2004. A case of intense predatory drilling of brachiopods from the Middle Miocene of southeastern Poland. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 214, 85–95. <https://doi.org/10.1016/j.palaeo.2004.07.023>.
- Baumiller, T.K., Gahn, F.J., 2002. Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid-crinoid interaction. *Paleontol. Soc. Pap.* 8, 195–210. <https://doi.org/10.1017/S1089332600001091>.
- Baumiller, T.K., Gahn, F.J., 2003. Predation on crinoids. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 263–278. https://doi.org/10.1007/978-1-4615-0161-9_11.
- Baumiller, T.K., Gahn, F.J., 2004. Testing predator-driven evolution with Paleozoic crinoid arm regeneration. *Science* 305, 1453–1455. <https://doi.org/10.1126/science.1101009>.
- Baumiller, T.K., Gahn, F.J., 2018. The nature of the platyceratid-crinoid association as revealed by cross-sectional data from the Carboniferous of Alabama (USA). *Swiss J. Paleontol.* 137, 177–187. <https://doi.org/10.1007/s13358-018-0167-8>.
- Baumiller, T.K., Macurda, D.B., 1995. Borings in Devonian and Mississippian blastoids (Echinodermata). *J. Paleontol.* 69, 1084–1089. <https://doi.org/10.1017/S0022336000038075>.
- Baumiller, T.K., Messing, C.G., 2007. Stalked crinoid locomotion, and its ecological and evolutionary implications. *Palaeontol. Electron.* 10.1.2A 1–10. https://palaeo-electronica.org/2007_1/crinoid/index.html.
- Baumiller, T.K., Leighton, L.R., Thompson, D.L., 1999. Boreholes in Mississippian spiriferide brachiopods and their implications for Paleozoic gastropod drilling. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 147, 283–289. [https://doi.org/10.1016/S0031-0182\(98\)00165-5](https://doi.org/10.1016/S0031-0182(98)00165-5).
- Baumiller, T.K., Bitner, M.A., Emig, C., 2006. High frequency of drill holes in brachiopods from the Pliocene of Algeria and its ecological implications. *Lethaia* 39, 313–320. <https://doi.org/10.1080/00241160600847546>.
- Baumiller, T.K., Mooi, R., Messing, C.G., 2008. Urchins in the meadow: Paleobiological and evolutionary implications of cidaroid predation on crinoids. *Paleobiology* 34, 22–34. <https://doi.org/10.1666/07031.1>.
- Baumiller, T.K., Marinovic, J.C., Tuura, M.E., Damstra, E.S., Miller, D.J., 2010a. Signs of boring predation on Middle Devonian hyolithids from the Michigan Basin. *PALAIOS* 25, 636–641. <https://doi.org/10.2110/palo.2010.p10-044r>.
- Baumiller, T.K., Salamon, M.A., Gorzelak, P., Mooi, R., Messing, C.G., Gahn, F.J., 2010b. Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution. *Proc. Natl. Acad. Sci.* 107, 5893–5896. <https://doi.org/10.1073/pnas.0914199107>.
- Becker-Kerber, B., Pacheco, M.L.A.F., Rudnitski, I.D., Galante, D., Rodrigues, F., Leme, J. de M., 2017. Ecological interactions in *Cloudina* from the Ediacaran of Brazil: implications for the rise of animal biomineralization. *Sci. Rep.* 7, 5482. <https://doi.org/10.1038/s41598-017-05753-8>.
- Behrens, E.W., Watson, R.L., 1969. Differential sorting of pelecypod valves in the swash zone. *J. Sediment. Res.* 39, 159–165. <https://doi.org/10.1306/74D71C03-2B21-11D7-8648000102C1865D>.
- Bence, J.R., Murdoch, W.W., 1986. Prey size selection by the mosquitofish: relation to optimal diet theory. *Ecology* 67, 324–336. <https://doi.org/10.2307/1938576>.
- Bengtson, S., 1968. The problematic genus *Mobergella* from the Lower Cambrian of the Baltic area. *Lethaia* 1, 325–351. <https://doi.org/10.1111/j.1502-3931.1968.tb01625.x>.
- Bengtson, S., Zhao, Y., 1992. Predatorial borings in late Precambrian mineralized exoskeletons. *Science* 257, 367–369. <https://doi.org/10.1126/science.257.5068.367>.
- Berg, C.J., 1976. Ontogeny of predatory behavior in marine snails (Prosobranchia: Naticidae). *The Nautilus* 90, 1–4.
- Berg, C.J., 1978. Development and evolution of behavior in mollusks, with emphasis on changes in stereotypy. In: Burghardt, G.M., Bekoff, M. (Eds.), *The Development of Behavior: Comparative and Evolutionary Aspects*. Garland STPM Press, New York, pp. 3–17.
- Berg, C.J., Nishenko, S., 1975. Stereotypy of predatory boring behavior of Pleistocene naticid gastropods. *Paleobiology* 1, 258–260. <https://doi.org/10.1017/S0094837300002517>.
- Bergström, J., 1973. Organization, life, and systematics of trilobites. *Foss. Strata* 2, 1–69.
- Berkyová, S., Fryda, J., Lukes, P., 2007. Unsuccessful predation on Middle Paleozoic plankton: Shell injury and anomalies in Devonian dacryonarid tentaculites. *Acta Palaeontol. Pol.* 52, 407–412.
- Berning, B., 2008. Evidence for sublethal predation and regeneration among living and fossil asaphoran bryozoans. In: Hageman, S.J., Key, M.M.J., Winston, J.E. (Eds.), *Bryozoan Studies 2007*, Virginia Museum of Natural History Special Publication 15. Virginia Museum of Natural History, Martinsville, pp. 1–5.
- Beu, A.G., 2008. Recent deep-water Cassidae of the world. A revision of *Galeodea*, *Oocorys*, *Sconsia*, *Echinophoria* and related taxa, with new genera and species (Mollusca, Gastropoda). *Mém. Muséum Natl. Hist. Nat.* 196, 269–387.
- Beu, A.G., Henderson, R.A., Nelson, C.S., 1972. Notes on the taphonomy and paleoecology of New Zealand Tertiary Spatangoida. *N. Z. J. Geol. Geophys.* 15, 275–286. <https://doi.org/10.1080/00288306.1972.10421961>.
- Beukema, J.J., 1968. Predation by the three-spined stickleback (*Gasterosteus aculeatus* L.): the influence of hunger and experience. *Behaviour* 31, 1–125. <https://doi.org/10.1163/156853968X00018>.
- Bhatia, S.B., Sirjana, Bajpai, S., 1989. Predation by gastropod drills on early Lutetian ostracods from Kutch, Western India. *Geobios* 22, 387–394. [https://doi.org/10.1016/S0016-6995\(89\)80138-X](https://doi.org/10.1016/S0016-6995(89)80138-X).
- Bianucci, G., Sorce, B., Storai, T., Landini, W., 2010. Killing in the Pliocene: Shark attack on a dolphin from Italy. *Palaeontology* 53, 457–470. <https://doi.org/10.1111/j.1475-4983.2010.00945.x>.
- Bibby, R., Cleall-Harding, P., Rundle, S., Widdicombe, S., Spicer, J., 2007. Ocean acidification disrupts induced defences in the intertidal gastropod *Littorina littorea*. *Biol. Lett.* 3, 699–701. <https://doi.org/10.1098/rsbl.2007.0457>.
- Bicknell, R., Pates, S., Botton, M., 2018. Abnormal xiphosurids, with possible application

- to Cambrian trilobites. *Palaeontol. Electron.* 21.2.19A 1–17. <https://doi.org/10.26879/866>.
- Bishop, G.A., 1972. Crab bitten by a fish from the Upper Cretaceous Pierre Shale of South Dakota. *Geol. Soc. Am. Bull.* 83, 3823–3826. [https://doi.org/10.1130/0016-7606\(1972\)83\[3823:CBAFFJ\]2.0.CO;2](https://doi.org/10.1130/0016-7606(1972)83[3823:CBAFFJ]2.0.CO;2).
- Bishop, G.A., 1975. Traces of predation. In: Frey, R.W. (Ed.), *The Study of Trace Fossils, a Synthesis of Principles, Problems and Procedures in Ichthyology*. Springer, New York, pp. 261–281.
- Bjork, P.R., 1981. Food habits of mosasaurs from the Pierre Shale of South Dakota. *Geol. Soc. Am. Abstr. Programs Rocky Mt. Sect.* 13, 191.
- Blake, D.B., Elliott, D.R., 2003. Ossicular homologies, systematics, and phylogenetic implications of certain North American Carboniferous asteroids (Echinodermata). *J. Paleontol.* 77, 476–489. <https://doi.org/10.1017/S002233600004419X>.
- Blake, D.B., Guensburg, T.E., 1994. Predation by the Ordovician asteroid *Promopalaeaster* on a pelecypod. *Lethaia* 27, 235–239. <https://doi.org/10.1111/j.1502-3931.1994.tb01415.x>.
- Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C., Finnegan, S., 2013. Climate change and the past, present, and future of biotic interactions. *Science* 341, 499–504. <https://doi.org/10.1126/science.1237184>.
- Blustein, D.H., Anderson, R.C., 2016. Localization of octopus drill holes on cowries. *Am. Malacol. Bull.* 34, 61–64. <https://doi.org/10.4003/006.034.0101>.
- Boessenecker, R.W., Perry, F.A., 2011. Mammalian bite marks on juvenile fur seal bones from the late Neogene Purisima Formation of Central California. *PALAIOS* 26, 115–120. <https://doi.org/10.2110/palo.2010.p10-088r>.
- Bohannon, B.J.M., Lenski, R.E., 2000. The relative importance of competition and predation varies with productivity in a model community. *Am. Nat.* 156, 329–340. <https://doi.org/10.1086/303393>.
- Bond, P.N., Saunders, W.B., 1989. Sublethal injury and shell repair in upper Mississippian ammonoids. *Paleobiology* 15, 414–428. <https://doi.org/10.1017/S0094837300009593>.
- Bottjer, D.J., Ausich, W.L., 1986. Phanerozoic development of tiering in soft substrata suspension-feeding communities. *Paleobiology* 12, 400–420. <https://doi.org/10.1017/S0094837300003134>.
- Bottjer, D.J., Jablonski, D., 1988. Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. *PALAIOS* 3, 540–560. <https://doi.org/10.2307/3514444>.
- Boucot, A.J., 1990. *Evolutionary Paleobiology of Behavior and Coevolution*. Elsevier, Amsterdam.
- Boucot, A.J., Brace, W.F., DeMar, R.E., 1958. Distribution of brachiopod and pelecypod shells by currents. *J. Sediment. Res.* 28, 321–332.
- Bowsher, A.L., 1955. Origin and adaptation of platyteratid gastropods. *Univ. Kans. Paleontol. Contrib. Mollusca* 5, 1–11.
- Brachanec, T., Lach, R., Salamon, M.A., Brom, K.R., 2017. Echinoid bite traces on Late Cretaceous (early Maastrichtian) sea lilies from southern Poland. *Paleontol. Res.* 21, 1–6. <https://doi.org/10.2517/2016PR015>.
- Brain, C.K., 2001. Some observations on *Cloudina*, a terminal Proterozoic index fossil from Namibia. *J. Afr. Earth Sci.* 33, 475–480. [https://doi.org/10.1016/S0899-5362\(01\)00083-5](https://doi.org/10.1016/S0899-5362(01)00083-5).
- Brandt, D.S., Meyer, D.L., Lask, P.B., 1995. *Isotelus* (Trilobita) “hunting burrow” from Upper Ordovician strata, Ohio. *J. Paleontol.* 69, 1079–1083. <https://doi.org/10.1017/S0022336000038063>.
- Breitbart, D.L., Steinberg, N., DuBeau, S., Cooksey, C., Houde, E.D., 1994. Effects of low dissolved oxygen on predation on estuarine fish larvae. *Mar. Ecol. Prog. Ser.* 104, 235–246.
- Brenchley, P.J., Newall, G., 1970. Flume experiments on the orientation and transport of models and shell valves. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 7, 185–220. [https://doi.org/10.1016/0031-0182\(70\)90093-3](https://doi.org/10.1016/0031-0182(70)90093-3).
- Breton, G., 1992. Les Goniasteridae (Asteroidea, Echinodermata) jurassiques et crétacées de France: taphonomie, systématique, paléogéographie, évolution. *Bull. Trimest. Soc. Géologie Normandie Amis Mus. Havre* 78, 1–590.
- Breton, G., Wisshak, M., Néraudeau, D., Morel, N., 2017. Parasitic gastropod bioerosion trace fossil on Cenomanian oysters from Le Mans, France and its ichnologic and taphonomic context. *Acta Palaeontol. Pol.* 62, 45–57. <https://doi.org/10.4202/app.00304.2016>.
- Brett, C.E., 1977. Entombment of a trilobite within a closed brachiopod shell. *J. Paleontol.* 51, 1041–1045.
- Brett, C.E., 1985. *Tremichnus*: a new ichnogenus of circular-parabolic pits in fossil echinoderms. *J. Paleontol.* 59, 625–635.
- Brett, C.E., 2003. Durophagous predation in Paleozoic marine benthic assemblages. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator-Prey Interactions in the Fossil Record*. Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 401–432. https://doi.org/10.1007/978-1-4615-0161-9_18.
- Brett, C.E., Walker, S.E., 2002. Predators and predation in Paleozoic marine environments. *Paleontol. Soc. Pap.* 8, 93–118. <https://doi.org/10.1017/S1089332600001078>.
- Brett, C.E., Zambito, J.J., Hunda, B.R., Schindler, E., 2012. Mid-Paleozoic trilobite Lagerstätten: models of diagenetically enhanced obrution deposits. *PALAIOS* 27, 326–345. <https://doi.org/10.2110/palo.2011.p11-040r>.
- Brezina, S.S., Cech, N., Martín Serrallta, D., Casadio, S., 2016. Cannibalism in Naticidae from the La Meseta Formation (Eocene, Antarctica). *Antarct. Sci.* 28, 205–215. <https://doi.org/10.1017/S0954102015000656>.
- Briffa, M., De la Haye, K., Munday, P.L., 2012. High CO₂ and marine animal behaviour: potential mechanisms and ecological consequences. *Mar. Pollut. Bull.* 64, 1519–1528. <https://doi.org/10.1016/j.marpolbul.2012.05.032>.
- Briggs, D.E.G., Rolfe, W.D.I., 1983. New Concavacarida (new order: ?Crustacea) from the Upper Devonian of Gogo, Western Australia, and the palaeoecology and affinities of the group. *Spec. Pap. Palaeontol.* 30, 249–276.
- Briggs, D.E.G., Erwin, D.H., Collier, F.J., 1994. *The Fossils of the Burgess Shale*. Smithsonian Institution Press, Washington, D.C. and London.
- Briggs, D.E.G., Rolfe, W.D.I., Butler, P.D., Liston, J.J., Ingham, J.K., 2011. Phyllocarid crustaceans from the Upper Devonian Gogo Formation, Western Australia. *J. Syst. Palaeontol.* 9, 399–424. <https://doi.org/10.1080/14772019.2010.493050>.
- Broda, K., Wolny, M., Zatoń, M., 2015. Palaeobiological significance of damaged and fragmented thylacocephalan carapaces from the Upper Devonian of Poland. *Proc. Geol. Assoc.* 126, 589–598. <https://doi.org/10.1016/j.pgeola.2015.05.005>.
- Broda, K., Collette, J., Budil, P., 2018. Phyllocarid crustaceans from the Late Devonian of the Kowala quarry (Holy Cross Mountains, Central Poland). *Pap. Palaeontol.* 4, 67–84. <https://doi.org/10.1002/spp2.1099>.
- Brom, K., 2014. Abrasion-induced holes in the bivalve shells from the Baltic Sea: implications for palaeontological studies. *Geosci. Notes* 2, 9–14.
- Brom, K.R., Oguri, K., Oji, T., Salamon, M.A., Gorzelak, P., 2018. Experimental neoichnology of crawling stalked crinoids. *Swiss J. Paleontol.* 137, 197–203. <https://doi.org/10.1007/s13358-018-0158-9>.
- Bromley, R.G., 1970. Borings as trace fossils and *Entobia cretacea* Portlock, as an example. *Geol. J. Spec. Issue* 3, 49–90.
- Bromley, R.G., 1981. Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geológica Hispánica* 16, 55–64.
- Bromley, R.G., 1993. Predation habits of octopus past and present and a new ichnospecies, *Oichnus ovalis*. *Bull. Geol. Soc. Den.* 40, 167–173.
- Bromley, R.G., 1996. *Trace Fossils: Biology, Taxonomy and Applications*. Chapman and Hall, London.
- Bromley, R.G., Pemberton, S.G., Rahmani, R.A., 1984. A Cretaceous woodground: the *Teredolites* ichnofossils. *J. Paleontol.* 58, 488–498.
- Brown, B., 1904. Stomach stones and food of plesiosaurs. *Science* 20, 184–185. <https://doi.org/10.1126/science.20.501.184>.
- Brown, K.M., Alexander, J.E., 1994. Group foraging in a marine gastropod predator: Benefits and costs to individuals. *Mar. Ecol. Prog. Ser.* 112, 97–105.
- Brown, K.M., Haight, E.S., 1992. The foraging ecology of the Gulf of Mexico stone crab *Menippe adina* (Williams et Felder). *J. Exp. Mar. Biol. Ecol.* 160, 67–80. [https://doi.org/10.1016/0022-0981\(92\)90111-M](https://doi.org/10.1016/0022-0981(92)90111-M).
- Buckland, W., 1858. The bridgewater treatises on the power, wisdom and goodness of God as manifested in the Creation. Treatise VI: Geology and Mineralogy Considered with Reference to Natural Theology, Third edition. .
- Bulkeley, B.T., 1968. Shell damage and repair in five members of the genus *Acmaea*. *The Veliger* 11, 64–66.
- Burrell, V.G., 1975. One oyster's solution to the drill problem. *The Veliger* 17, 334.
- Bush, A.M., Bambach, R.K., 2011. Paleoeccologic megatrends in marine Metazoa. *Annu. Rev. Earth Planet. Sci.* 39, 241–269. <https://doi.org/10.1146/annurev-earth-040809-152556>.
- Butterfield, N.J., 2002. *Leanochoilia* guts and the interpretation of three-dimensional structures in Burgess Shale-type fossils. *Paleobiology* 28, 155–171. [https://doi.org/10.1666/0094-8373\(2002\)028<0155:LGATIO>2.0.CO;2](https://doi.org/10.1666/0094-8373(2002)028<0155:LGATIO>2.0.CO;2).
- Cadée, G.C., 1994. Eider, shelduck, and other predators, the main producers of shell fragments in the Wadden Sea: palaeoecological implications. *Palaeontology* 37, 181–202.
- Cadée, G.C., 1995. Birds as producers of shell fragments in the Wadden Sea, in particular the role of the Herring gull. *Geobios* 28, 77–85. [https://doi.org/10.1016/S0016-6995\(95\)80155-3](https://doi.org/10.1016/S0016-6995(95)80155-3).
- Cadée, G.C., 1999. Shell damage and shell repair in the Antarctic limpet *Nacella concinna* from King George Island. *J. Sea Res.* 41, 149–161.
- Cadée, G.C., 2011. *Hydrobia* as “Jonah in the whale”: Shell repair after passing through the digestive tract of shelducks alive. *PALAIOS* 26, 245–249. <https://doi.org/10.2110/palo.2010.p10-095r>.
- Cadée, G.C., 2016. Rolling cockles: Shell abrasion and repair in a living bivalve *Cerastoderma edule* L. *Ichnos* 23, 180–188. <https://doi.org/10.1080/10420940.2016.1164152>.
- Cadée, G.C., Walker, S.E., Flessa, K.W., 1997. Gastropod shell repair in the intertidal of Bahía la Choya (N. Gulf of California). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 136, 67–78. [https://doi.org/10.1016/S0031-0182\(97\)00041-2](https://doi.org/10.1016/S0031-0182(97)00041-2).
- Campbell, D.C., Campbell, L.D., Campbell, M.R., Portell, R.W., 1997. Distribution and paleoecology of *Glottidia inexpectans* Olsson, 1914 (Brachiopoda: Lingulidae). *Tulane Stud. Geol. Paleontol.* 30, 159–170.
- Canfield, D.E., 2005. The early history of atmospheric oxygen: Homage to Robert M. Garrels. *Annu. Rev. Earth Planet. Sci.* 33, 1–36. <https://doi.org/10.1146/annurev-earth.33.092203.122711>.
- Capellini, G., 1865. *Balenottere Fossili del Bolognese*. Tipi Gamberini e Parmeggiani, Bologna.
- Carlson Jones, D., 2003. *Bivalve Epibiont Armor: the Evolution of an Antipredatory Strategy* (Dissertation). University of Cincinnati, Cincinnati, Ohio.
- Carney, R.S., 2005. Zonation of deep biota on continental margins. *Oceanogr. Mar. Biol. Annu. Rev.* 43, 221–288.
- Carriker, M.R., 1951. Observations on the penetration of tightly closing bivalves by *Busycos* and other predators. *Ecology* 32, 73–83. <https://doi.org/10.2307/1930973>.
- Carriker, M.R., 1998. Predatory gastropod traces: a comparison of verified shallow-water and presumed deep-sea boreholes. *Am. Malacol. Bull.* 14, 121–131.
- Carriker, M.R., Gruber, G.L., 1999. Uniqueness of the gastropod accessory boring organ (ABO): Comparative biology, an update. *J. Shellfish Res.* 18, 579–595.
- Carriker, M.R., Yochelson, E.L., 1968. Recent gastropod boreholes and Ordovician cylindrical borings. *Geol. Surv. Prof. Pap.* 593-B, 1–26 5 pls.
- Case, T.J., 2000. *An Illustrated Guide to Theoretical Ecology*. Oxford University Press, New York.

- Casey, M.M., Chattopadhyay, D., 2008. Clumping behavior as a strategy against drilling predation: Implications for the fossil record. *J. Exp. Mar. Biol. Ecol.* 367, 174–179. <https://doi.org/10.1016/j.jembe.2008.09.020>.
- Casey, M.M., Dietl, G.P., Post, D.M., Briggs, D.E.G., 2014. The impact of eutrophication and commercial fishing on molluscan communities in Long Island Sound, USA. *Biol. Conserv.* 170, 137–144. <https://doi.org/10.1016/j.biocon.2013.12.037>.
- Casey, M.M., Farrell, U.C., Dietl, G.P., Villeux, D.J., 2015. Mixed assemblages of drilling predators and the problem of identity in the fossil record: a case study using the muricid gastropod *Ecphora*. *Paleobiology* 41, 680–696. <https://doi.org/10.1017/pab.2015.32>.
- Casey, M.M., Fall, L.M., Dietl, G.P., 2016. You are what you eat: Stable isotopic evidence indicates that the naticid gastropod *Neverita duplicata* is an omnivore. *Front. Ecol. Evol.* 4, 125. <https://doi.org/10.3389/fevo.2016.00125>.
- Caster, K.E., Kjellesvig-Waering, E.N., 1964. Upper Ordovician eurypterids of Ohio. *Palaeontogr. Am.* 4 (32), 301–358.
- Ceranka, T., Zlotnik, M., 2003. Traces of cassid snails predation upon the echinoids from the Middle Miocene of Poland. *Acta Palaeontol. Pol.* 48, 491–496.
- Charnov, E.L., 1976. Optimal foraging: Attack strategy of a mantid. *Am. Nat.* 110, 141–151. <https://doi.org/10.1086/283054>.
- Chattopadhyay, D., Bala, T., 2013. Effect of lithification on drilling predation: an experimental approach. *Geol. Soc. Am. Abstr. Programs* 45, 316.
- Chattopadhyay, D., Baumiller, T.K., 2007. Drilling under threat: an experimental assessment of the drilling behavior of *Nucella lamellosa* in the presence of a predator. *J. Exp. Mar. Biol. Ecol.* 352, 257–266. <https://doi.org/10.1016/j.jembe.2007.08.001>.
- Chattopadhyay, D., Baumiller, T.K., 2010. Effect of durophagy on drilling predation: a case study of Cenozoic molluscs from North America. *Hist. Biol.* 22, 367–379. <https://doi.org/10.1080/08912961003600445>.
- Chattopadhyay, D., Dutta, S., 2013. Prey selection by drilling predators: a case study from Miocene of Kutch, India. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 374, 187–196. <https://doi.org/10.1016/j.palaeo.2013.01.016>.
- Chattopadhyay, D., Rathie, A., Das, A., 2013a. The effect of morphology on postmortem transportation of bivalves and its taphonomic implications. *PALAIOS* 28, 203–209. <https://doi.org/10.2110/palo.2012.p12-103r>.
- Chattopadhyay, D., Rathie, A., Miller, D.J., Baumiller, T.K., 2013b. Hydrodynamic effects of drill holes on postmortem transportation of bivalve shells and its taphonomic implications. *PALAIOS* 28, 875–884. <https://doi.org/10.2110/palo.2013.029>.
- Chattopadhyay, D., Sarkar, D., Dutta, S., Prasanjit, S.R., 2014a. What controls cannibalism in drilling gastropods? A case study on *Natica tigrina*. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 410, 126–133. <https://doi.org/10.1016/j.palaeo.2014.05.037>.
- Chattopadhyay, D., Zuschin, M., Tomašových, A., 2014b. Effects of a high-risk environment on edge-drilling behavior: inference from Recent bivalves from the Red Sea. *Paleobiology* 40, 34–49. <https://doi.org/10.1666/13024>.
- Chattopadhyay, D., Zuschin, M., Tomašových, A., 2015. How effective are ecological traits against drilling predation? Insights from recent bivalve assemblages of the northern Red Sea. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 440, 659–670. <https://doi.org/10.1016/j.palaeo.2015.09.047>.
- Chattopadhyay, D., Zuschin, M., Dominici, S., Sawyer, J.A., 2016. Patterns of drilling predation in relation to stratigraphy, locality and sieve size: Insights from the Eocene molluscan fauna of the Paris Basin. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 459, 86–98. <https://doi.org/10.1016/j.palaeo.2016.07.001>.
- Checa, A., 1993. Non-predatory shell damage in Recent deep-endobenthic bivalves from Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 100, 309–331. [https://doi.org/10.1016/0031-0182\(93\)90061-M](https://doi.org/10.1016/0031-0182(93)90061-M).
- Chen, J.Y., Zhou, G.Q., 1997. Biology of the Chengjiang fauna. *Bull. Natl. Mus. Nat. Sci.* 10, 11–105.
- Cherns, L., Wright, V.P., 2000. Missing molluscs as evidence of large-scale, early skeletal aragonite dissolution in a Silurian sea. *Geology* 28, 791–794. [https://doi.org/10.1130/0091-7613\(2000\)28<791:MMAEOL>2.0.CO;2](https://doi.org/10.1130/0091-7613(2000)28<791:MMAEOL>2.0.CO;2).
- Cherns, L., Wright, V.P., 2009. Quantifying the impacts of early diagenetic aragonite dissolution on the fossil record. *PALAIOS* 24, 756–771. <https://doi.org/10.2110/palo.2008.p08-134r>.
- Cherns, L., Wheeley, J.R., Wright, V.P., 2010. Taphonomic bias in shelly faunas through time: early aragonite dissolution and its implications for the fossil record. In: Allison, P.A., Bottjer, D.J. (Eds.), *Taphonomy, Topics in Geobiology*. Springer, Dordrecht, pp. 79–105. https://doi.org/10.1007/978-90-481-8643-3_3.
- Chiba, T., Sato, S., 2012. Size-selective predation and drillhole-site selectivity in *Euspira fortunei* (Gastropoda: Naticidae): Implications for ecological and palaeoecological studies. *J. Molluscan Stud.* 78, 205–212. <https://doi.org/10.1093/mollus/ey002>.
- Chiba, T., Sato, S., 2016. Climate-mediated changes in predator–prey interactions in the fossil record: a case study using shell-drilling gastropods from the Pleistocene Japan Sea. *Paleobiology* 42, 257–268. <https://doi.org/10.1017/pab.2015.38>.
- Chin, K., 2002. Analyses of coprolites produced by carnivorous vertebrates. *Paleontol. Soc. Pap.* 8, 43–50. <https://doi.org/10.1017/S1089332600001042>.
- Chiu, J.M.Y., Shin, P.K.S., Wong, K.-P., Cheung, S.-G., 2010. Sibling cannibalism in juveniles of the marine gastropod *Nassarius festivus* (Powys, 1835). *Malacologia* 52, 157–161. <https://doi.org/10.4002/040.052.0109>.
- Chojnacki, N.C., Leighton, L.R., 2014. Comparing predatory drillholes to taphonomic damage from simulated wave action on a modern gastropod. *Hist. Biol.* 26, 69–79. <https://doi.org/10.1080/08912963.2012.758118>.
- Choo, B., Long, J.A., Trinajstić, K., 2009. A new genus and species of basal actinopterygian fish from the Upper Devonian Gogo Formation of Western Australia. *Acta Zool.* 90, 194–210. <https://doi.org/10.1111/j.1463-6395.2008.00370.x>.
- Cicimurri, D.J., Everhart, M.J., 2001. An elasmosaur with stomach contents and gastroliths from the Pierre Shale (Late Cretaceous) of Kansas. *Trans. Kans. Acad. Sci.* 104, 129–143.
- Cintra-Buenrostro, C.E., 2007. Trampling, peeling and nibbling mussels: an experimental assessment of mechanical and predatory damage to shells of *Mytilus trossulus* (Mollusca: Mytilidae). *J. Shellfish Res.* 26, 221–231. [https://doi.org/10.2983/0730-8000\(2007\)26\[221:TPANMA\]2.0.CO;2](https://doi.org/10.2983/0730-8000(2007)26[221:TPANMA]2.0.CO;2).
- Cintra-Buenrostro, C.E., Flessa, K.W., Avila-Serrano, G., 2005. Who cares about a vanishing clam? Trophic importance of *Mulinia coloradoensis* inferred from predatory damage. *PALAIOS* 20, 296–302. <https://doi.org/10.2110/palo.2004.p04-21>.
- Claeson, K.M., Sarr, R., Hill, R.V., Sow, E.H., Malou, R., O'Leary, M.A., 2015. New fossil scombrid (Pelagia: Scombridae) fishes preserved as predator and prey from the Eocene of Senegal. *Proc. Acad. Nat. Sci. Phila.* 164, 133–147. <https://doi.org/10.1635/053.164.0111>.
- Clarke, J.M., 1908. The beginnings of dependent life. *Bull. N. Y. State Mus.* 121, 1–28.
- Clarke, J.M., 1912. Early adaptation in the feeding habits of star-fishes. *J. Acad. Nat. Sci. Phila.* 2 (15), 113–118.
- Clarkson, E.N.K., Henry, J.-L., 1973. Structures coaptatives et enroulement chez quelques Trilobites ordoviéniens et siluriens. *Lethaia* 6, 105–132. <https://doi.org/10.1111/j.1502-3931.1973.tb01186.x>.
- Clarkson, M.O., Kasemann, S.A., Wood, R.A., Lenton, T.M., Daines, S.J., Richoz, S., Ohnemüller, F., Meixner, A., Poulton, S.W., Tipper, E.T., 2015. Ocean acidification and the Permian-Triassic mass extinction. *Science* 348, 229–232. <https://doi.org/10.1126/science.aaa0193>.
- Clements, J.C., Hunt, H.L., 2015. Marine animal behaviour in a high CO₂ ocean. *Mar. Ecol. Prog. Ser.* 536, 259–279. <https://doi.org/10.3354/meps11426>.
- Clements, J.C., Hunt, H.L., 2017. Effects of CO₂-driven sediment acidification on infaunal marine bivalves: a synthesis. *Mar. Pollut. Bull.* 117, 6–16. <https://doi.org/10.1016/j.marpolbul.2017.01.053>.
- Clements, J.C., Rawlings, T.A., 2014. Ontogenetic shifts in the predatory habits of the northern moon snail (*Lunatia heros*) on the northwestern Atlantic coast. *J. Shellfish Res.* 33, 755–768. <https://doi.org/10.2983/035.033.0310>.
- Clements, J.C., Coffin, M.R.S., Lavaud, R., Guyondet, T., Comeau, L., 2018. Ocean acidification and molluscan shell taphonomy: can elevated seawater pCO₂ influence taphonomy in a naticid predator–prey system? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 507, 145–154. <https://doi.org/10.1016/j.palaeo.2018.07.007>.
- Cohen, P.A., Riedman, L.A., 2018. It's a protist-eat-protist world: Recalcitrance, predation, and evolution in the Tonian–Cryogenian ocean. *Emerg. Top. Life Sci.* 2, 173–180. <https://doi.org/10.1042/ETLS20170145>.
- Collareta, A., Landini, W., Lambert, O., Post, K., Tinelli, C., Di Celma, C., Panetta, D., Tripodi, M., Salvadori, P.A., Caramella, D., Marchi, D., Urbina, M., Bianucci, G., 2015. Piscivory in a Miocene Cetotheriidae of Peru: first record of fossilized stomach content for an extinct baleen-bearing whale. *Sci. Nat.* 102, 70. <https://doi.org/10.1007/s00114-015-1319-y>.
- Collareta, A., Lambert, O., Landini, W., Di Celma, C., Malinverno, E., Varas-Malca, R., Urbina, M., Bianucci, G., 2017a. Did the giant extinct shark *Carcharocles megalodon* target small prey? Bite marks on marine mammal remains from the Late Miocene of Peru. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 469, 84–91. <https://doi.org/10.1016/j.palaeo.2017.01.001>.
- Collareta, A., Landini, W., Chacaltana, C., Valdivia, W., Altamirano-Sierra, A., Urbina-Schmitt, M., Bianucci, G., 2017b. A well preserved skeleton of the fossil shark *Cosmopolitodus hastalis* from the Late Miocene of Peru, featuring fish remains as fossilized stomach contents. *Riv. Ital. Paleontol. e Stratigr.* 123, 11–22.
- Collen, J.D., 1973. Morphology and development of the test surface in some species of *Notorotalia* (Foraminifera). *Rev. Esp. Micropaleontol.* 5, 113–132.
- Conway Morris, S., 1979. The Burgess Shale (Middle Cambrian) Fauna. *Annu. Rev. Ecol. Syst.* 10, 327–349. <https://doi.org/10.1146/annurev.es.10.110179.001551>.
- Conway Morris, S., 1990. *Typhloesus wellsi* (Melton and Scott, 1973), a bizarre metazoan from the Carboniferous of Montana, U.S.A. *Philos. Trans. R. Soc. B Biol. Sci.* 327, 595–624. <https://doi.org/10.1098/rstb.1990.0102>.
- Conway Morris, S., Jenkins, R.J.F., 1985. Healed injuries in Early Cambrian trilobites from South Australia. *Alcheringa* 9, 167–177. <https://doi.org/10.1080/03115518508618965>.
- Conway Morris, S., Robison, R.A., 1986. Middle Cambrian priapulids and other soft-bodied fossils from Utah and Spain. *Univ. Kans. Paleontol. Contrib.* 117, 1–22.
- Conway Morris, S., Robison, R.A., 1988. More soft-bodied animals and algae from the Middle Cambrian of Utah and British Columbia. *Univ. Kans. Paleontol. Contrib.* 122, 1–48.
- Coovert, G.A., Coovert, H.K., 1995. Revision of the supraspecific classification of marginelliform gastropods. *The Nautilus* 109, 43–110.
- Cope, E.D., 1868. Remarks on a new enaliosaurian, *Elasmosaurus platyrus*. *Proc. Acad. Nat. Sci. Phila.* 20, 92–93.
- Cope, E.D., 1871. Synopsis of the Extinct Batrachia, Reptilia and Aves of North America: Part I. McCalla & Stavelly Printers, Philadelphia.
- Cope, E.D., 1872. On a species of *Clidastes* and on *Plesiosaurus gulo* Cope. *Proc. Acad. Nat. Sci. Phila.* 29, 127–129.
- Cronin, K.E., Dietl, G.P., Kelley, P.H., Edie, S.M., 2018. Lifespan bias explains live-dead discordance in abundance of two common bivalves. *Paleobiology* 44, 783–797. <https://doi.org/10.1017/pab.2018.32>.
- Culotta, E., 1988. *Predators and Available Prey: Naticid Predation during a Neogene Molluscan Extinction Event*. University of Michigan, Ann Arbor, Michigan.
- Culver, S.J., Lipps, J.H., 2003. Predation on and by Foraminifera. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator–Prey Interactions in the Fossil Record*. Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 7–32. https://doi.org/10.1007/978-1-4615-0161-9_2.
- Daley, A.C., 2008. Statistical analysis of mixed-motive shell borings in Ordovician, Silurian, and Devonian brachiopods from northern and eastern Canada. *Can. J. Earth Sci.* 45, 213–229. <https://doi.org/10.1139/E07-061>.

- Daley, G.M., Ostrowski, S., Geary, D.H., 2007. Paleoenvironmentally correlated differences in a classic predator-prey system: the bivalve *Chione elevata* and its gastropod predators. *PALAIOS* 22, 166–173. <https://doi.org/10.2110/palo.2005.p05-057r>.
- Das, T., Stickle, W.B., 1993. Sensitivity of crabs *Callinectes sapidus* and *C. similis* and the gastropod *Stramonita haemastoma* to hypoxia and anoxia. *Mar. Ecol. Prog. Ser.* 98, 263–274. <https://doi.org/10.3354/meps098263>.
- Das, S., Chattopadhyay, Devapriya, Chattopadhyay, Debarati, 2015. The effect of hunger on drilling behaviour of *Natica tigrina*: an experimental assessment. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 429, 57–61. <https://doi.org/10.1016/j.palaeo.2015.04.007>.
- Davidson, R.G., Trewin, N.H., 2005. Unusual preservation of the internal organs of acanthodian and actinopterygian fish in the Middle Devonian of Scotland. *Scott. J. Geol.* 41, 129–134. <https://doi.org/10.1144/sjg41020129>.
- Davis, R.A., Fraaye, R.H.B., Holland, C.H., 2001. Trilobites within nautiloid cephalopods. *Lethaia* 34, 37–45. <https://doi.org/10.1080/002411601300068251>.
- Dawkins, R., Krebs, J.R., 1979. Arms races between and within species. *Proc. R. Soc. B Biol. Sci.* 205, 489–511. <https://doi.org/10.1098/rspb.1979.0081>.
- Day, R.W., Barkai, A., Wickens, P.A., 1991. Trapping of three drilling whelks by two species of mussel. *J. Exp. Mar. Biol. Ecol.* 149, 109–122. [https://doi.org/10.1016/0022-0981\(91\)90119-H](https://doi.org/10.1016/0022-0981(91)90119-H).
- De Cauwer, G., 1985. Gastropod predation on corbulid bivalves. *Palaeoecology or taphonomy?* *Soc. R. Zool. Belg. Ann.* 115, 183–196.
- Deline, B., 2008. The first evidence of predatory or parasitic drilling in stylophoran echinoderms. *Acta Palaeontol. Pol.* 53, 739–743.
- Deline, B., Baumiller, T., Kaplan, P., Kowalewski, M., Hoffmeister, A.P., 2003. Edge-drilling on the brachiopod *Perditocardinia* cf. *P. dubia* from the Mississippian of Missouri (USA). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 201, 211–219. [https://doi.org/10.1016/S0031-0182\(03\)00626-6](https://doi.org/10.1016/S0031-0182(03)00626-6).
- Delsett, L.L., Novis, L.K., Roberts, A.J., Koevoets, M.J., Hammer, Ø., Druckenmiller, P.S., Hurum, J.H., 2016. The Slottsmøya marine reptile *Lagerstätte*: depositional environments, taphonomy and diagenesis. *Geol. Soc. Lond. Spec. Publ.* 434, 165–188. <https://doi.org/10.1144/SP434.2>.
- Deméré, T.A., Cerutti, R.A., 1982. A Pliocene shark attack on a cethotheriid whale. *J. Paleontol.* 56, 1480–1482.
- Denison, R.H., 1956. A review of the habitat of the earliest vertebrates. *Fieldiana Geol.* 11, 361–457.
- Dennis, K., Miles, R.S., 1981. A pachyosteorhynchid arthrodire from Gogo, Western Australia. *Zool. J. Linnean Soc.* 73, 213–258. <https://doi.org/10.1111/j.1096-3642.1981.tb01594.x>.
- D'Hondt, S., Pilson, M.E.Q., Sigurdsson, H., Hanson, A.K., Carey, S., 1994. Surface-water acidification and extinction at the Cretaceous-Tertiary boundary. *Geology* 22, 983–986. [https://doi.org/10.1130/0091-7613\(1994\)022<0983:SWAAEA>2.3.CO;2](https://doi.org/10.1130/0091-7613(1994)022<0983:SWAAEA>2.3.CO;2).
- Dietl, G.P., 2002. Traces of naticid predation on the gryphaeid oyster *Pycnodonte dissimularis*: Epifaunal drilling of prey in the Paleocene. *Hist. Biol.* 16, 13–19. <https://doi.org/10.1080/0891296021000041764>.
- Dietl, G.P., 2003a. Interaction strength between a predator and dangerous prey: *Sinistrofulgur* predation on *Mercenaria*. *J. Exp. Mar. Biol. Ecol.* 289, 287–301. [https://doi.org/10.1016/S0022-0981\(03\)00047-9](https://doi.org/10.1016/S0022-0981(03)00047-9).
- Dietl, G.P., 2003b. Coevolution of a marine gastropod predator and its dangerous bivalve prey. *Biol. J. Linn. Soc.* 80, 409–436. <https://doi.org/10.1046/j.1095-8312.2003.00255.x>.
- Dietl, G.P., 2004. Origins and circumstances of adaptive divergence in whelk feeding behavior. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 208, 279–291. <https://doi.org/10.1016/j.palaeo.2004.03.011>.
- Dietl, G.P., Alexander, R.A., 1995. Borehole site and prey size stereotypy in naticid predation on *Euspira* (*Lunatia*) *heros* (Say, 1822) and *Neverita* (*Polinices*) *duplicata* (Say, 1822) from the southern New Jersey coast. *J. Shellfish Res.* 14, 307–314.
- Dietl, G.P., Alexander, R.R., 1997. Predator-prey interactions between the naticids *Euspira heros* Say and *Neverita duplicata* Say and the Atlantic surfclam *Spisula solidissima* Dillwyn from Long Island to Delaware. *J. Shellfish Res.* 16, 413–422.
- Dietl, G.P., Alexander, R.R., 1998. Shell repair frequencies in whelks and moon snails from Delaware and southern New Jersey. *Malacologia* 39, 151–165.
- Dietl, G.P., Alexander, R.R., 2000. Post-Miocene shift in stereotypic naticid predation on conchiferal prey from the mid-Atlantic shelf: Coevolution with dangerous prey. *PALAIOS* 15, 414–429. [https://doi.org/10.1669/0883-1351\(2000\)015<0414:PMSISN>2.0.CO;2](https://doi.org/10.1669/0883-1351(2000)015<0414:PMSISN>2.0.CO;2).
- Dietl, G.P., Kelley, P.H., 2002. The fossil record of predator-prey arms races: Coevolution and escalation hypotheses. *Paleontol. Soc. Pap.* 8, 353–374. <https://doi.org/10.1017/S1089332600001157>.
- Dietl, G.P., Kelley, P.H., 2006. Can naticid gastropod predators be identified by the holes they drill? *Ichnos* 13, 103–108. <https://doi.org/10.1080/10420940600848889>.
- Dietl, G.P., Kosloski, M.E., 2013. On the measurement of repair frequency: how important is data standardization? *PALAIOS* 28, 394–402. <https://doi.org/10.2110/palo.2012.p12-076r>.
- Dietl, G.P., Alexander, R.R., Bien, W.F., 2000. Escalation in Late Cretaceous–early Paleocene oysters (Gryphaeidae) from the Atlantic Coastal Plain. *Paleobiology* 26, 215–237. [https://doi.org/10.1666/0094-8373\(2000\)026<0215:EILCEP>2.0.CO;2](https://doi.org/10.1666/0094-8373(2000)026<0215:EILCEP>2.0.CO;2).
- Dietl, G.P., Herbert, G.S., Vermeij, G.J., 2004. Reduced competition and altered feeding behavior among marine snails after a mass extinction. *Science* 306, 2229–2231. <https://doi.org/10.1126/science.1106182>.
- Dietl, G.P., Nagel-Myers, J., Aronson, R.B., 2018. Indirect effects of climate change altered the cannibalistic behaviour of shell-drilling gastropods in Antarctica during the Eocene. *R. Soc. Open Sci.* 5, 181446. <https://doi.org/10.1098/rsos.181446>.
- Dodd, J.R., Stanton, R.J., 1990. *Paleoecology: Concepts and Applications*, 2nd ed. Wiley, New York.
- Dollo, L., 1887. Le hainosaure et les nouveaux vertébrés fossiles du Musée de Bruxelles. *Rev. Quest. Sci.* 22, 70–112.
- Doney, S.C., Fabry, V.J., Feely, R.A., Kleypas, J.A., 2009. Ocean acidification: the other CO₂ problem. *Annu. Rev. Mar. Sci.* 1, 169–192. <https://doi.org/10.1146/annurev.marine.010908.163834>.
- Donovan, S.K., Novak, V., 2015. Site selectivity of predatory borings in Late Pliocene balanid barnacles from south-east Spain. *Lethaia* 48, 1–3. <https://doi.org/10.1111/let.12077>.
- Douglas, R.G., 1973. Benthonic foraminiferal biostratigraphy in the central North Pacific, Leg 17, Deep Sea Drilling Project. Initial Rep. Deep Sea Drill. Proj. 17, 607–671.
- Driscoll, E.G., 1967. Experimental field study of shell abrasion. *J. Sediment. Res.* 37, 1117–1123. <https://doi.org/10.1306/74D71843-2B21-11D7-8648000102C1865D>.
- Driscoll, E.G., 1970. Selective bivalve shell destruction in marine environments; a field study. *J. Sediment. Res.* 40, 898–905. <https://doi.org/10.1306/74D720DB-2B21-11D7-8648000102C1865D>.
- Dudley, E.C., Vermeij, G.J., 1978. Predation in time and space: Drilling in the gastropod *Turritella*. *Paleobiology* 4, 436–441. <https://doi.org/10.1017/S0094837300006175>.
- Dyer, A.D., Ellis, E.R., Molinaro, D.J., Leighton, L.R., 2018. Experimental fragmentation of gastropod shells by sediment compaction: Implications for interpreting drilling predation intensities in the fossil record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 511, 332–340. <https://doi.org/10.1016/j.palaeo.2018.08.018>.
- Dzik, J., 1981. Origin of the Cephalopoda. *Acta Palaeontol. Pol.* 26, 161–191.
- Eastman, C.R., 1964. IV. Jurassic saurian remains ingested within fish. *Ann. Carnegie Mus.* 8, 182–187.
- Ebbestad, J.O.R., Tapanila, L., 2005. Non-predatory borings in *Phanerotrema* (Gastropoda), Early Silurian, Anticosti Island, Québec, Canada. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 221, 325–341. <https://doi.org/10.1016/j.palaeo.2005.03.003>.
- Ebbestad, J.O.R., Lindström, A., Peel, J.S., 2009. Predation on bellerophonitiform molluscs in the Palaeozoic. *Lethaia* 42, 469–485. <https://doi.org/10.1111/j.1502-3931.2009.00167.x>.
- Ebert, M., Kölbl-Ebert, M., Lane, J.A., 2015. Fauna and predator-prey relationships of Ettling, an actinopterygian fish-dominated Konservat-Lagerstätte from the Late Jurassic of Southern Germany. *PLoS One* 10, e0116140. <https://doi.org/10.1371/journal.pone.0116140>.
- Ebling, F.J., Kitching, J.A., Muntz, L., Taylor, C.M., 1964. The ecology of Lough Ine: III. Experimental observations of the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. *J. Anim. Ecol.* 33, 73–82. <https://doi.org/10.2307/2349>.
- Edgecombe, G.D., Chatterton, B.D.E., 1987. An operculum of the Silurian nautiloid *Aptychopsis* from Arctic Canada. *Lethaia* 20, 63–65. <https://doi.org/10.1111/j.1502-3931.1987.tb00760.x>.
- Edwards, D.C., 1969. Predators on *Olivella biplicata*, including a species-specific predator avoidance response. *The Veliger* 11, 326–333.
- Edwards, D.C., Huebner, J.D., 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. *Ecology* 58, 1218–1236. <https://doi.org/10.2307/1935077>.
- Edwards, C.T., Saltzman, M.R., Royer, D.L., Fike, D.A., 2017. Oxygenation as a driver of the Great Ordovician Biodiversification Event. *Nat. Geosci.* 10, 925–929. <https://doi.org/10.1038/s41561-017-0006-3>.
- Ehret, D.J., MacFadden, B.J., Salas-Gismondi, R., 2009. Caught in the act: Trophic interactions between a 4-million-year-old white shark (*Carcharodon*) and mysticete whale from Peru. *PALAIOS* 24, 329–333. <https://doi.org/10.2110/palo.2008.p08-077r>.
- Elliott, D.R., 2008. Sponge predation by a Mississippian asteroid and feeding behaviors, food selection, and feeding habits of fossil asteroids. *Trans. Mo. Acad. Sci.* 42, 14–17. <https://doi.org/10.30956/0544-540X-42.2008.14>.
- Eriksson, P.G., Banerjee, S., Catuneanu, O., Corcoran, P.L., Eriksson, K.A., Hiatt, E.E., Laflamme, M., Lenhardt, N., Long, D.G.F., Miall, A.D., Mints, M.V., Pufahl, P.K., Sarkar, S., Simpson, E.L., Williams, G.E., 2013. Secular changes in sedimentation systems and sequence stratigraphy. *Gondwana Res.* 24, 468–489. <https://doi.org/10.1016/j.jgr.2012.09.008>.
- Ernst, G., 1967. Über Fossilnester in *Pachydiscus*-Gehäusen und das Lagenvorkommen von Echiniden in der Oberkreide NW-Deutschlands. *Paläontol. Z.* 41, 211–229. <https://doi.org/10.1007/BF02988124>.
- Ernsting, G., 1977. Effects of food deprivation and type of prey on predation by *Notiophilus biguttatus* F. (Carabidae) on springtails (Collembola). *Oecologia* 31, 13–20. <https://doi.org/10.1007/BF00348704>.
- Esteve, J., Hughes, N.C., Zamora, S., 2011. Purujosa trilobite assemblage and the evolution of trilobite enrollment. *Geology* 39, 575–578. <https://doi.org/10.1130/G31985.1>.
- Esteve, J., Rubio, P., Zamora, S., Rahman, I.A., 2017. Modelling enrolment in Cambrian trilobites. *Paleontology* 60, 423–432. <https://doi.org/10.1111/pala.12294>.
- Everhart, M.J., 2008. A bitten skull of *Tylosaurus kansansensis* (Squamata: Mosasauridae) and a review of mosasaur-on-mosasaur pathology in the fossil record. *Trans. Kans. Acad. Sci.* 111, 251–262.
- Fahlke, J.M., 2012. Bite marks revisited - evidence for middle-to-late Eocene *Basilosaurus* predation on *Dorudon atrox* (both Cetacea, Basilosauridae). *Palaeontol. Electron.* 15.3.32A 1–16. <https://doi.org/10.26879/341>.
- Fatka, O., Budil, P., 2014. Sheltered gregarious behavior of Middle Ordovician harpetid trilobites. *PALAIOS* 29, 495–500. <https://doi.org/10.2110/palo.2013.031>.
- Fatka, O., Vokac, V., Moravec, J., Sinagl, M., Valent, M., 2009. Agnostids entombed in hyolith conchs. *Mem. Assoc. Australas. Palaeontol.* 37, 481–489.
- Feldmann, R.M., Quilty, P.G., 1997. First Pliocene decapod crustacean (Malacostraca: Palinuridae) from the Antarctic. *Antarct. Sci.* 9, 56–60.
- Fell, H.B., 1966. The ecology of ophiuroids. In: Booloontan, R.A. (Ed.), *Physiology of Echinodermata*. Interscience Publishers, New York, pp. 129–143.

- Ferrari, M.C.O., McCormick, M.I., Munday, P.L., Meekan, M.G., Dixon, D.L., Lonnstedt, Ö., Chivers, D.P., 2011. Putting prey and predator into the CO₂ equation - qualitative and quantitative effects of ocean acidification on predator-prey interactions: CO₂-induced change in consumptive effects. *Ecol. Lett.* 14, 1143–1148. <https://doi.org/10.1111/j.1461-0248.2011.01683.x>.
- Fike, D.A., Grotzinger, J.P., Pratt, L.M., Summons, R.E., 2006. Oxidation of the Ediacaran Ocean. *Nature* 444, 744–747. <https://doi.org/10.1038/nature05345>.
- Fischer, P.H., 1966. Perforations de fossiles Tertiaires par des gastéropodes prédateurs. *J. Conchyliol.* 106, 66–96.
- Forcino, F.L., Stafford, E.S., Tetreault, R.L., 2017. Brachiopod morphology, life mode, and crushing predation in the Ordovician Arnheim Formation, Kentucky, USA. *Hist. Biol.* <https://doi.org/10.1080/08912963.2017.1407929>.
- Forel, M.-B., Ozsvárt, P., Moix, P., 2018. Carnian (Late Triassic) ostracods from the Sorgun Ophiolitic Mélange (Southern Turkey): Taxonomy, palaeoenvironment, and evidence of predation. *Palaeontol. Electron.* 21.2.26A 1–23. <https://doi.org/10.26879/852>.
- Fortunato, H., 2007. Naticid gastropod predation in the Gatun Formation (late Middle Miocene), Panama: preliminary assessment. *Paläontol. Z.* 81, 356–364. <https://doi.org/10.1007/BF02990184>.
- Fraaije, R.H.B., 2003. The oldest in situ hermit crab from the Lower Cretaceous of Speeton, UK. *Palaeontology* 46, 53–57.
- Fraaije, R.H.B., Pennings, H.W.J., 2006. Crab carapaces preserved in nautiloid shells from the Upper Paleocene of Huesca (Pyrenees, Spain). *Rev. Mex. Cienc. Geológicas* 23, 361–363.
- Fraaije, R.H.B., López-Horgue, M., Bruce, N.L., Van Bakel, B.W.M., Jagt, J.W.M., Klompmaker, A.A., 2019. New isopod and achelatan crustaceans from mid-Cretaceous reefal limestones in the Basque-Cantabrian Basin, northern Spain. *Cretaceous Research*.
- Fraaye, R.H.B., 1996. Late Cretaceous swimming crabs: Radiation, migration, competition, and extinction. *Acta Geol. Pol.* 46, 269–278.
- Fraaye, R., Jäger, M., 1995a. Decapods in ammonite shells: examples of inquilinism from the Jurassic of England and Germany. *Palaeontology* 38, 63–76.
- Fraaye, R.H.B., Jäger, M., 1995b. Ammonite inquilinism by fishes: examples from the Lower Jurassic of Germany and England. *Neues Jahrb. für Geol. Paläontol. Monatshefte* 9, 541–552.
- Fregeau, M.R., 1991. The Trophic Ecology of *Lunatia heros* and its Competitive Interactions with *Polinices duplicatus* (Dissertation). University of Massachusetts, Amherst.
- Frey, R.W., Dörjes, J., 1988. Fair-and foul-weather shell accumulations on a Georgia beach. *PALAIOS* 3, 561–576. <https://doi.org/10.2307/3514445>.
- Frey, R.W., Henderson, S.W., 1987. Left-right phenomena among bivalve shells: examples from the Georgia coast. *Senckenberg. Maritima* 19, 223–247.
- Fürsich, F.T., Jablonski, D., 1984. Late Triassic naticid drillholes: Carnivorous gastropods gain a major adaptation but fail to radiate. *Science* 224, 78–80. <https://doi.org/10.1126/science.224.4644.78>.
- Furuhashi, T., Schwarzing, C., Miksik, I., Smrz, M., Beran, A., 2009. Molluscan shell evolution with review of shell calcification hypothesis. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* 154, 351–371. <https://doi.org/10.1016/j.cbpb.2009.07.011>.
- Futterer, E., 1982. Experiments on the distinction of wave and current influenced shell accumulations. In: Einsele, G., Seilacher, A. (Eds.), *Cyclic and Event Stratification*. Springer, Berlin, Heidelberg, pp. 175–179. https://doi.org/10.1007/978-3-642-75829-4_12.
- Gaemers, P.A.M., Langeveld, B.W., 2015. Attempts to predate on gadid fish otoliths demonstrated by naticid gastropod drill holes from the Neogene of Mill-Langenboom, The Netherlands. *Scr. Geol.* 149, 159–183.
- Gahn, F.J., Baumiller, T.K., 2003. Infestation of Middle Devonian (Givetian) camerate crinoids by platyceratid gastropods and its implications for the nature of their biotic interaction. *Lethaia* 36, 71–82. <https://doi.org/10.1080/00241160310003072>.
- Gahn, F.J., Baumiller, T.K., 2005. Arm regeneration in Mississippian crinoids: evidence of intense predation pressure in the Paleozoic? *Paleobiology* 31, 151–164. [https://doi.org/10.1666/0094-8373\(2005\)031<0151:ARIMCE>2.0.CO;2](https://doi.org/10.1666/0094-8373(2005)031<0151:ARIMCE>2.0.CO;2).
- Gahn, F.J., Baumiller, T.K., 2006. Using platyceratid gastropod behaviour to test functional morphology. *Hist. Biol.* 18, 397–404. <https://doi.org/10.1080/08912960600668524>.
- Gale, A.S., Sørensen, A.M., 2015. Origin of the balanomorph barnacles (Crustacea, Cirripedia, Thoracica): new evidence from the Late Cretaceous (Campanian) of Sweden. *J. Syst. Palaeontol.* 13, 791–824. <https://doi.org/10.1080/14772019.2014.954824>.
- Gale, A.S., Kennedy, W.J., Martill, D., 2017. Mosasauroid predation on an ammonite – *Pseudaspisidoceras* – from the Early Turonian of south-eastern Morocco. *Acta Geol. Pol.* 67, 31–46. <https://doi.org/10.1515/aggp-2017-0003>.
- Galindo, L.A., Puillandre, N., Utge, J., Lozouet, P., Bouchet, P., 2016. The phylogeny and systematics of the Nassariidae revisited (Gastropoda, Buccinoidea). *Mol. Phylogenet. Evol.* 99, 337–353. <https://doi.org/10.1016/j.ympev.2016.03.019>.
- Galle, A., Finner, F., 2004. Middle Devonian *Calceola sandalina* (Linnaeus, 1771) (Anthozoa, Rugosa) from Moravia (Czech Republic): aspects of functional morphology, gerontic growth patterns, and epibionts. *Geodiversitas* 26, 17–31.
- Galle, A., Mikuláš, R., 2003. Evidence of predation on the rugose coral *Calceola sandalina* (Devonian, Czech Republic). *Ichnos* 10, 41–45. <https://doi.org/10.1080/10420940390235107>.
- Ganić, M., Radović, P., Rundić, L., Bradić, K., Knežević, S., 2016. Traces of drilling predation in the Badenian mollusks from the Rakovica stream (Belgrade, Serbia). *Geol. Croat.* 69, 205–212.
- Garton, D., Stickle, W.B., 1980. Effects of salinity and temperature on the predation rate of *Thais haemastoma* on *Crassostrea virginica* spat. *Biol. Bull.* 158, 49–57. <https://doi.org/10.2307/1540757>.
- Gašparič, R., Fraaije, R.H.B., Van Bakel, B.W.M., Jagt, J.W.M., Skupien, P., 2015. Mesozoic-Cenozoic crustaceans preserved within echinoid tests and bivalve shells. *Bull. Geosci.* 90, 601–611. <https://doi.org/10.3140/bull.geosci.1551>.
- Geary, D.H., Allmon, W.D., Reaka-Kudla, M.L., 1991. Stomatopod predation on fossil gastropods from the Plio-Pleistocene of Florida. *J. Paleontol.* 65, 355–360. <https://doi.org/10.1017/S0022336000030341>.
- German, C.R., Ramirez-Llodra, E., Baker, M.C., Tyler, P.A., ChEES Scientific Steering Committee, 2011. Deep-water chemosynthetic ecosystem research during the census of marine life decade and beyond: a proposed deep-ocean road map. *PLoS One* 6, e23259. <https://doi.org/10.1371/journal.pone.0023259>.
- Gibson, M.A., Watson, J.B., 1989. Predatory and non-predatory borings in echinoids from the upper Ocala Formation (Eocene), North-Central Florida, U.S.A. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 71, 309–321. [https://doi.org/10.1016/0031-0182\(89\)90058-8](https://doi.org/10.1016/0031-0182(89)90058-8).
- Gingras, M.K., Armitage, I.A., Pemberton, S.G., Clifton, H.E., 2007. Pleistocene walrus herds in the Olympic Peninsula area: Trace-fossil evidence of predation by hydraulic jetting. *PALAIOS* 22, 539–545. <https://doi.org/10.2110/palo.2005.p05-120r>.
- Godwin, M., 1998. Palaeoenvironments and cyclicity of the Beeston Chalk (Upper Campanian) in Norfolk and their possible links with the nektonic palaeoecology of *Belemnites*. *Bull. Geol. Soc. Norfolk* 47, 23–60.
- Gordillo, S., 2013a. Muricid boreholes in Pleistocene acorn barnacles from the Beagle Channel: trophic interactions during the Last Interglacial in southern South America. *Alcheringa* 37, 479–486. <https://doi.org/10.1080/03115518.2013.792458>.
- Gordillo, S., 2013b. Cannibalism in Holocene muricid snails in the Beagle Channel, at the extreme southern tip of South America: an opportunistic response? *Palaeontol. Electron.* 16.1.4A 1–13. <https://doi.org/10.26879/344>.
- Gordillo, S., Archuby, F., 2012. Predation by drilling gastropods and asteroids upon mussels in rocky shallow shores of southernmost South America: Paleontological implications. *Acta Palaeontol. Pol.* 57, 633–646. <https://doi.org/10.4202/app.2010.0116>.
- Goźelak, P., Salamon, M.A., 2013. Experimental tumbling of echinoderms - Taphonomic patterns and implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 386, 569–574. <https://doi.org/10.1016/j.palaeo.2013.06.023>.
- Goźelak, P., Niedźwiedzki, G., Skawina, A., 2010. Pathologies of non-marine bivalve shells from the Late Triassic of Poland. *Lethaia* 43, 285–289. <https://doi.org/10.1111/j.1502-3931.2009.00188.x>.
- Goźelak, P., Salamon, M.A., Baumiller, T.K., 2012. Predator-induced macroevolutionary trends in Mesozoic crinoids. *Proc. Natl. Acad. Sci.* 109, 7004–7007. <https://doi.org/10.1073/pnas.1201573109>.
- Goźelak, P., Salamon, M.A., Trzęsiok, D., Niedźwiedzki, R., 2013. Drill holes and predation traces versus abrasion-induced artifacts revealed by tumbling experiments. *PLoS One* 8, e58528. <https://doi.org/10.1371/journal.pone.0058528>.
- Gosselin, L.A., Chia, F.-S., 1996. Prey selection by inexperienced predators: do early juvenile snails maximize net energy gains on their first attack? *J. Exp. Mar. Biol. Ecol.* 199, 45–58. [https://doi.org/10.1016/0022-0981\(95\)00190-5](https://doi.org/10.1016/0022-0981(95)00190-5).
- Gould, S.J., Vrba, E.S., 1982. Exaptation - a missing term in the science of form. *Paleobiology* 8, 4–15. <https://doi.org/10.1017/S0094837300004310>.
- Grey, M., 2001. Predator-Prey Relationships of Naticid Gastropods and their Bivalve Prey (MS Thesis). University of Guelph, Guelph.
- Grey, M., Boulding, E.G., Brookfield, M.E., 2005. Shape differences among boreholes drilled by three species of naticid gastropods. *J. Molluscan Stud.* 71, 253–256. <https://doi.org/10.1093/mollus/eyi035>.
- Grey, M., Boulding, E.G., Brookfield, M.E., 2006. Estimating multivariate selection gradients in the fossil record: a naticid gastropod case study. *Paleobiology* 32, 100–108. [https://doi.org/10.1666/0094-8373\(2006\)032\[0100:EMSGIT\]2.0.CO;2](https://doi.org/10.1666/0094-8373(2006)032[0100:EMSGIT]2.0.CO;2).
- Griffiths, D., 1980. Foraging costs and relative prey size. *Am. Nat.* 116, 743–752. <https://doi.org/10.1086/283666>.
- Gripp, K., 1929. Über Verletzungen an Seeigeln aus der Kreide Norddeutschlands. *Paläontol. Z.* 11, 238–245. <https://doi.org/10.1007/BF03042728>.
- Grun, T.B., 2016. Echinoid test damage by a stingray predator. *Lethaia* 49, 285–286. <https://doi.org/10.1111/let.12165>.
- Grun, T.B., 2017. Recognizing traces of snail predation on the Caribbean sand dollar *Leodia sexiesperforata*. *PALAIOS* 32, 448–461. <https://doi.org/10.2110/palo.2017.001>.
- Grun, T., Sievers, D., Nebelsick, J.H., 2014. Drilling predation on the clypeasteroid echinoid *Echinocyamus pusillus* from the Mediterranean Sea (Giglio, Italy). *Hist. Biol.* 26, 745–757. <https://doi.org/10.1080/08912963.2013.841683>.
- Grun, T.B., Kroh, A., Nebelsick, J.H., 2017. Comparative drilling predation on time-averaged phosphatized and nonphosphatized assemblages of the minute clypeasteroid echinoid *Echinocyamus stellatus* from Miocene offshore sediments (Globigerina Limestone Formation, Malta). *J. Paleontol.* 91, 633–642. <https://doi.org/10.1017/jpa.2016.123>.
- Guerrero, S., Reymont, R.A., 1988. Predation and feeding in the naticid gastropod *Naticarius intricatoides* (Hidalgo). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 68, 49–52. [https://doi.org/10.1016/0031-0182\(88\)90015-6](https://doi.org/10.1016/0031-0182(88)90015-6).
- Hagadorn, J.W., Boyajian, G.E., 1997. Subtle changes in mature predator-prey systems; an example from Neogene *Turritella* (Gastropoda). *PALAIOS* 12, 372–379. <https://doi.org/10.2307/3515336>.
- Hagdorn, H., 1998. Triassic Ophiuroids (*Aspiduriella*) brooding in an empty ceratite shell. In: Candia Carnevali, M.D., Bonasoro, F. (Eds.), *Echinoderm Research*. Balkema, Rotterdam p. 278.
- Hageman, S.A., Kaesler, R.L., 2002. Fusulinids: predation damage and repair of tests from the Upper Pennsylvanian of Kansas. *J. Paleontol.* 76, 181–184. [https://doi.org/10.1666/0022-3360\(2002\)076<0181:FPDARO>2.0.CO;2](https://doi.org/10.1666/0022-3360(2002)076<0181:FPDARO>2.0.CO;2).
- Hagstrom, K.M., 1996. Effects of Compaction and Wave-Induced Forces on the Preservation and Macroevolutionary Perception of Naticid Predator-Prey Interactions

- (MS Thesis). Indiana University, Bloomington.
- Hallock, P., Talge, H.K., 1994. A predatory foraminifer, *Floresina amphiphaga*, n. sp., from the Florida Keys. *J. Foraminif. Res.* 24, 210–213.
- Hallock, P., Talge, H.K., Williams, D.E., Harney, J.N., 1998. Borings in *Amphistegina* (Foraminifera): evidence of predation by *Floresina amphiphaga* (Foraminifera). *Hist. Biol.* 13, 73–76. <https://doi.org/10.1080/08912969809386574>.
- Hanks, J.E., 1957. The rate of feeding of the common oyster drill, *Urosalpinx cinerea* (Say), at controlled water temperatures. *Biol. Bull.* 112, 330–335.
- Hansen, T.A., Kelley, P.H., 1995. Spatial variation of naticid gastropod predation in the Eocene of North America. *PALAIOS* 10, 268–278.
- Hansen, M.C., Mapes, R.H., 1990. A predator-prey relationship between sharks and cephalopods in the late Paleozoic. In: Boucot, A.J. (Ed.), *Evolutionary Paleobiology of Behaviour and Coevolution*. Elsevier, Amsterdam, pp. 189–192.
- Harley, C.D.G., 2011. Climate change, keystone predation, and biodiversity loss. *Science* 334, 1124–1127. <https://doi.org/10.1126/science.1210199>.
- Harper, E.M., 1991. The role of predation in the evolution of cementation in bivalves. *Palaeontology* 34, 455–460.
- Harper, E.M., 1994. Are conchiolin sheets in corbulid bivalves primarily defensive? *Palaeontology* 37, 551–578.
- Harper, E.M., 2006. Dissecting post-Palaeozoic arms races. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 232, 322–343. <https://doi.org/10.1016/j.palaeo.2005.05.017>.
- Harper, E.M., Kelley, P.H., 2012. Treatise Online no. 44: part N, revised, volume 1, chapter 22: Predation of bivalves. *Treat. Online* 21.
- Harper, E.M., Peck, L.S., 2016. Latitudinal and depth gradients in marine predation pressure. *Glob. Ecol. Biogeogr.* 25, 670–678. <https://doi.org/10.1111/geb.12444>.
- Harper, E.M., Skelton, P.W., 1993a. The Mesozoic marine revolution and epifaunal bivalves. *Scr. Geol. Spec. Issue* 2, 127–153.
- Harper, E.M., Skelton, P.W., 1993b. A defensive value of the thickened periostracum in the Mytiloidea. *The Veliger* 36, 36–42.
- Harper, E.M., Wharton, D.S., 2000. Boring predation and Mesozoic articulate brachiopods. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 158, 15–24. [https://doi.org/10.1016/S0031-0182\(99\)00164-9](https://doi.org/10.1016/S0031-0182(99)00164-9).
- Harper, E.M., Forsythe, G.T., Palmer, T., 1998. Taphonomy and the Mesozoic marine revolution; preservation state masks the importance of boring predators. *PALAIOS* 13, 352–360.
- Harper, E.M., Peck, L.S., Hendry, K.R., 2009. Patterns of shell repair in articulate brachiopods indicate size constitutes a refuge from predation. *Mar. Biol.* 156, 1993–2000. <https://doi.org/10.1007/s00227-009-1230-1>.
- Harper, E.M., Clark, M.S., Hoffman, J.I., Philipp, E.E.R., Peck, L.S., Morley, S.A., 2012. Iceberg scour and shell damage in the Antarctic bivalve *Laternula elliptica*. *PLoS One* 7, e46341. <https://doi.org/10.1371/journal.pone.0046341>.
- Harper, E.M., Crame, J.A., Sogot, C.E., 2018. “Business as usual”: Drilling predation across the K-Pg mass extinction event in Antarctica. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 498, 115–126. <https://doi.org/10.1016/j.palaeo.2018.03.009>.
- Harris, G.F., 1897. *Catalogue of Tertiary Mollusca in the Department of Geology. Part 1. Australasia. Order of the Trustees*, London.
- Hart, M.W., Palmer, A.R., 1987. Stereotype, ontogeny, and heritability of drill site selection in thaidid gastropods. *J. Exp. Mar. Biol. Ecol.* 107, 101–120. [https://doi.org/10.1016/0022-0981\(87\)90189-4](https://doi.org/10.1016/0022-0981(87)90189-4).
- Harvey, B.P., Moore, P.J., 2017. Ocean warming and acidification prevent compensatory response in a predator to reduced prey quality. *Mar. Ecol. Prog. Ser.* 563, 111–122. <https://doi.org/10.3354/meps11956>.
- Haselmair, A., Stachowitsch, M., Zuschin, M., Riedel, B., 2010. Behaviour and mortality of benthic crustaceans in response to experimentally induced hypoxia and anoxia in situ. *Mar. Ecol. Prog. Ser.* 414, 195–208. <https://doi.org/10.3354/meps08657>.
- Hattori, K.E., Kelley, P.H., Dietl, G.P., Moore, N.O., Simpson, S.L., Zappulla, A.M., Ottens, K.J., Visaggi, C.C., 2014. Validation of taxon-specific sampling by novice collectors for studying drilling predation in fossil bivalves. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 412, 199–207. <https://doi.org/10.1016/j.palaeo.2014.07.034>.
- Hausmann, I.M., Domanski, H., Zuschin, M., 2018. Influence of setting, sieve size, and sediment depth on multivariate and univariate assemblage attributes of coral reef-associated mollusc death assemblages from the Gulf of Aqaba. *Facies* 64, 20. <https://doi.org/10.1007/s10347-018-0530-7>.
- Hawlena, D., Pérez-Mellado, V., 2009. Change your diet or die: Predator-induced shifts in insectivorous lizard feeding ecology. *Oecologia* 161, 411–419. <https://doi.org/10.1007/s00442-009-1375-0>.
- Hazlett, B.A., 1970. The effect of shell size and weight on the agonistic behavior of a hermit crab. *Z. für Tierpsychol.* 27, 369–374. <https://doi.org/10.1111/j.1439-0310.1970.tb01878.x>.
- Heck, K.L., Thoman, T.A., 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.* 53, 125–134. [https://doi.org/10.1016/0022-0981\(81\)90014-9](https://doi.org/10.1016/0022-0981(81)90014-9).
- Heller, R., 1980. On optimal diet in a patchy environment. *Theor. Popul. Biol.* 17, 201–214. [https://doi.org/10.1016/0040-5809\(80\)90006-4](https://doi.org/10.1016/0040-5809(80)90006-4).
- Hembree, D.I., Mapes, R.H., Goiran, C., 2014. The impact of high-energy storms on shallow-water *Nautilus* (Cephalopoda) taphonomy, Lifou (Loyalty Islands). *PALAIOS* 29, 348–362. <https://doi.org/10.2110/palo.2013.113>.
- Herbert, G.S., 2018. Evidence for intense biotic interactions in the eastern Gulf of Mexico after a two million year hiatus: inferences from muricid edge-drilling behaviour. *J. Molluscan Stud.* 84, 426–431. <https://doi.org/10.1093/mollus/eyy037>.
- Herbert, G.S., Dietl, G.P., Fortunato, H., Simone, L.R.L., Sliko, J., 2009. Extremely slow feeding in a tropical drilling ectoparasite, *Vitularia salebrosa* (King and Broderip, 1832) (Gastropoda: Muricidae), on molluscan hosts from Pacific Panama. *The Nautilus* 123, 121–136.
- Herbert, G.S., Whitenack, L.B., McKnight, J.Y., 2016. Behavioural versatility of the giant murex *Muricanthus fulvescens* (Sowerby, 1834) (Gastropoda: Muricidae) in interactions with difficult prey. *J. Molluscan Stud.* 82, 357–365. <https://doi.org/10.1093/mollus/eyw013>.
- Herrero, C., Canales, M.L., 2002. Taphonomic processes in selected Lower and Middle Jurassic Foraminifera from the Iberian Range and Basque-Cantabrian Basin (Spain). *J. Foraminif. Res.* 32, 22–42. <https://doi.org/10.2113/0320022>.
- Hess, H., 1960. Neubeschreibung von *Geocoma elegans* (Ophiuroidea) aus dem unteren Callovien von la Voulte-sur-Rhône (Ardèche). *Eclogae Geol. Helvetiae* 53, 335–385.
- Hill, R.V., Roberts, E.M., Tapanila, L., Bouaré, M.L., Sissoko, F., O’Leary, M.A., 2015. Multispecies shark feeding in the Trans-Saharan seaway: evidence from Late Cretaceous dyrosaurid (Crocodyliformes) fossils from northeastern Mali. *PALAIOS* 30, 589–596. <https://doi.org/10.2110/palo.2014.109>.
- Hiller, N., 2014. Drill holes and shell repair in brachiopods from a Late Cretaceous (Maastrichtian) oyster reef, North Canterbury, New Zealand. *Cretac. Res.* 49, 83–90. <https://doi.org/10.1016/j.cretres.2014.01.001>.
- Hlavín, W., 1990. Arthrodire-ctenacanth shark. In: Boucot, A.J. (Ed.), *Evolutionary Paleobiology of Behaviour and Coevolution*. Elsevier, Amsterdam, pp. 192–195.
- Hoegh-Guldberg, O., Cai, R., Poloczanska, E.S., Brewer, P.G., Sundby, S., Hilmi, K., Fabry, V.J., Jung, S., Skirving, W., Stone, D.A., 2014. The ocean. In: Barros, V.R., Field, C.B., Dokken, D.J., Mastrandrea, M.D., Mach, K.J., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects, Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp. 1655–1731.
- Hoffman, A., Martinelli, J., 1984. Prey selection by naticid gastropods in the Pliocene of Emporda (Northeast Spain). *Neues Jahrb. für Geol. Paläontol. Monatshft* 1984, 393–399.
- Hoffman, A., Pisera, A., Ryszkiewicz, M., 1974. Predation by muricid and naticid gastropods on the Lower Tortonian mollusks from the Korytnica clays. *Acta Geol. Pol.* 24, 249–260.
- Hoffmeister, A.P., Kowalewski, M., 2001. Spatial and environmental variation in the fossil record of drilling predation: a case study from the Miocene of Central Europe. *PALAIOS* 16, 566–579.
- Hoffmeister, A.P., Kowalewski, M., Bambach, R.K., Baumiller, T.K., 2003. Intense drilling in the Carboniferous brachiopod *Cardiaria cordata* Cooper, 1956. *Lethaia* 36, 107–117. <https://doi.org/10.1080/00241160310000408>.
- Hoffmeister, A.P., Kowalewski, M., Baumiller, T.K., Bambach, R.K., 2004. Drilling predation on Permian brachiopods and bivalves from the Glass Mountains, west Texas. *Acta Palaeontol. Pol.* 49, 443–454.
- Hofmann, G.E., Barry, J.P., Edmunds, P.J., Gates, R.D., Hutchins, D.A., Klinger, T., Sewell, M.A., 2010. The effect of ocean acidification on calcifying organisms in marine ecosystems: an organism-to-ecosystem perspective. *Annu. Rev. Ecol. Evol. Syst.* 41, 127–147. <https://doi.org/10.1146/annurev.ecolsys.110308.120227>.
- Holling, C.S., 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.* 91, 293–320. <https://doi.org/10.4039/Ent91293-5>.
- Holt, R.D., Grover, J., Tilman, D., 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am. Nat.* 144, 741–771. <https://doi.org/10.1086/285705>.
- Hönisch, B., Ridgwell, A., Schmidt, D.N., Thomas, E., Gibbs, S.J., Sluijs, A., Zeebe, R., Kump, L., Martindale, R.C., Greene, S.E., Kiessling, W., Ries, J., Zachos, J.C., Royer, D.L., Barker, S., Marchitto, T.M., Moyer, R., Pelejero, C., Ziveri, P., Foster, G.L., Williams, B., 2012. The geological record of ocean acidification. *Science* 335, 1058–1063. <https://doi.org/10.1126/science.1208277>.
- Hryniewicz, K., Amamo, A., Bitner, M.A., Hagström, J., Kiel, S., Klompmaker, A.A., Mörs, T., Robins, C.M., Kaim, A., 2019. A late Paleocene fauna from shallow-water chemosynthesis-based ecosystems, Spitsbergen, Svalbard. *Acta Palaeontol. Pol.* 64, 101–141. <https://doi.org/10.4202/app.00554.2018>.
- Hua, H., Pratt, B.R., Zhang, L.-Y., 2003. Borings in *Cloudina* shells: complex predator-prey dynamics in the terminal Neoproterozoic. *PALAIOS* 18, 454–459. [https://doi.org/10.1669/0883-1351\(2003\)018<0454:BICSCP>2.0.CO;2](https://doi.org/10.1669/0883-1351(2003)018<0454:BICSCP>2.0.CO;2).
- Hughes, R.N., Dunkin, S. de B., 1984. Behavioural components of prey selection by dogwhelks, *Nuccella lapillus* (L.), feeding on mussels, *Mytilus edulis* L., in the laboratory. *J. Exp. Mar. Biol. Ecol.* 77, 45–68. [https://doi.org/10.1016/0022-0981\(84\)90050-9](https://doi.org/10.1016/0022-0981(84)90050-9).
- Hughes, R.N., Elnor, R.W., 1989. Foraging behaviour of a tropical crab: *Calappa ocellata* Holthuis feeding upon the mussel *Brachidontes domingensis* (Lamarck). *J. Exp. Mar. Biol. Ecol.* 133, 93–101. [https://doi.org/10.1016/0022-0981\(89\)90160-3](https://doi.org/10.1016/0022-0981(89)90160-3).
- Hughes, R.N., Hughes, H.P.I., 1971. A study of the gastropod *Cassia tuberosa* (L.) preying upon sea urchins. *J. Exp. Mar. Biol. Ecol.* 7, 305–314.
- Hughes, R.N., Hughes, H.P.I., 1981. Morphological and behavioural aspects of feeding in the Cassidae (Tonnacea, Mesogastropoda). *Malacologia* 20, 385–402.
- Hunt, A.P., 1992. Late Pennsylvanian coprolites from the Kinney Brick Quarry, central New Mexico with notes on the classification and utility of coprolites. *N. M. Bur. Mines Miner. Resour. Bull.* 138, 221–229.
- Hunt, A.P., Lucas, S.G., 2014. Jurassic vertebrate bromalites of the western United States in the context of the global record. *Vol. Jurassica* 12, 151–158.
- Huntley, J.W., Kowalewski, M., 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. *Proc. Natl. Acad. Sci.* 104, 15006–15010. <https://doi.org/10.1073/pnas.0704960104>.
- Hutchings, J.A., Herbert, G.S., 2013. No honor among snails: conspecific competition leads to incomplete drill holes by a naticid gastropod. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 379–380, 32–38. <https://doi.org/10.1016/j.palaeo.2013.04.003>.
- Isida, S., 2005. Comparison of penetration costs and ingestion speeds among muricid gastropods with different foraging strategies. *The Veliger* 47, 163–168.
- Ishikawa, M., Kase, T., 2007. Multiple predatory drill holes in *Cardiolucina* (Bivalvia:

- Lucinidae): effect of conchiolin sheets in predation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 254, 508–522. <https://doi.org/10.1016/j.palaeo.2007.07.004>.
- Ishikawa, M., Kase, T., Tsutsui, H., Tojo, B., 2004. Snails versus hermit crabs: a new interpretation on shell-peeling predation in fossil gastropod assemblages. *Paleontol. Res.* 8, 99–108. <https://doi.org/10.2517/prpsj.8.99>.
- Ivany, L.C., Portell, R.W., Jones, D.S., 1990. Animal-plant relationships and paleobiogeography of an Eocene seagrass community from Florida. *PALAIOS* 5, 244–258. <https://doi.org/10.2307/3514943>.
- Jablonski, D., 2008. Biotic interactions and macroevolution: extensions and mismatches across scales and levels. *Evolution* 62, 715–739. <https://doi.org/10.1111/j.1558-5646.2008.00317.x>.
- Jäger, M., Fraaye, R., 1997. The diet of the early Toarcian ammonite *Harpoceras falci-ferum*. *Palaeontologia* 40, 557–574.
- Jagt, J.W.M., Van Bakel, B.W.M., Fraaije, R.H.B., Neumann, C., 2006. In situ fossil hermit crabs (Paguroidea) from northwest Europe and Russia: preliminary data on new records. *Rev. Mex. Cienc. Geológicas* 23, 364–369.
- Janvier, P., 1996. *Early Vertebrates*. Clarendon Press, Oxford.
- Jellison, B.M., Ninokawa, A.T., Hill, T.M., Sanford, E., Gaylord, B., 2016. Ocean acidification alters the response of intertidal snails to a key sea star predator. *Proc. R. Soc. B Biol. Sci.* 283, 20160890. <https://doi.org/10.1098/rspb.2016.0890>.
- Jensen, S., 1990. Predation by Early Cambrian trilobites on infaunal worms - evidence from the Swedish Mickwitzia Sandstone. *Lethaia* 23, 29–42. <https://doi.org/10.1111/j.1502-3931.1990.tb01779.x>.
- Johnsen, S.A.L., Ahmed, M., Leighton, L.R., 2013. The effect of spines of a Devonian productide brachiopod on durophagous predation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 375, 30–37. <https://doi.org/10.1016/j.palaeo.2013.02.009>.
- Johnson, R.G., 1957. Experiments on the burial of shells. *J. Geol.* 65, 527–535. <https://doi.org/10.1086/626453>.
- Johnson, E.H., Anderson, B.M., Allmon, W.D., 2017. What can we learn from all those pieces? Obtaining data on drilling predation from fragmented high-spined gastropod shells. *PALAIOS* 32, 271–277. <https://doi.org/10.2110/palo.2016.088>.
- Joyce, W.G., 2000. The first complete skeleton of *Solnhofia parsonsi* (Cryptodira, Eurysternidae) from the Upper Jurassic of Germany and its taxonomic implications. *J. Paleontol.* 74, 684–700. [https://doi.org/10.1666/0022-3360\(2000\)074<0684:TFCOS>2.0.CO;2](https://doi.org/10.1666/0022-3360(2000)074<0684:TFCOS>2.0.CO;2).
- Kabat, A.R., 1990. Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia* 32, 155–193.
- Kabat, A.R., Kohn, A.J., 1986. Predation on Early Pleistocene naticid gastropods in Fiji. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 53, 255–269. [https://doi.org/10.1016/0031-0182\(86\)90062-3](https://doi.org/10.1016/0031-0182(86)90062-3).
- Kaim, A., Sztajner, P., 2005. The opercula of neritopsid gastropods and their phylogenetic importance. *J. Molluscan Stud.* 71, 211–219. <https://doi.org/10.1093/mollus/eyi029>.
- Kallal, R.J., Godfrey, S.J., Ortner, D.J., 2012. Bone reactions on a Pliocene cetacean rib indicate short-term survival of predation event. *Int. J. Osteoarchaeol.* 22, 253–260. <https://doi.org/10.1002/oa.1199>.
- Kanie, Y., Fukuda, Y., Nakayama, H., Seki, K., Hattori, M., 1980. Implosion of living *Nautilus* under increased pressure. *Paleobiology* 6, 44–47. <https://doi.org/10.1017/S0094837300012483>.
- Kaplan, P., Baumiller, T.K., 2000. Taphonomic inferences on boring habit in the Richmondian *Onniella meeki* Epibole. *PALAIOS* 15, 499–510. [https://doi.org/10.1669/0883-1351\(2000\)015<0499:TIOBHI>2.0.CO;2](https://doi.org/10.1669/0883-1351(2000)015<0499:TIOBHI>2.0.CO;2).
- Kardon, G., 1998. Evidence from the fossil record of an antipredatory exaptation: conchiolin layers in corbulid bivalves. *Evolution* 52, 68–79. <https://doi.org/10.1111/j.1558-5646.1998.tb05139.x>.
- Kase, T., Ishikawa, M., 2003. Mystery of naticid predation history solved: evidence from a “living fossil” species. *Geology* 31, 403–406. [https://doi.org/10.1130/0091-7613\(2003\)031<0403:MONPHS>2.0.CO;2](https://doi.org/10.1130/0091-7613(2003)031<0403:MONPHS>2.0.CO;2).
- Kauffman, E.G., Kesling, R.V., 1960. An Upper Cretaceous ammonite bitten by a mosasaur. *Univ. Mich. Contrib. Mus. Paleontol.* 15, 193–248.
- Kaunzinger, C.M.K., Morin, P.J., 1998. Productivity controls food-chain properties in microbial communities. *Nature* 395, 495–497. <https://doi.org/10.1038/26741>.
- Kear, B.P., Godthelp, H., 2008. Inferred vertebrate bite marks on an Early Cretaceous unionoid bivalve from Lightning Ridge, New South Wales, Australia. *Alcheringa* 32, 65–71. <https://doi.org/10.1080/03115510701757498>.
- Kear, B.P., Boles, W.E., Smith, E.T., 2003. Unusual gut contents in a Cretaceous ichthyosaur. *Proc. R. Soc. Lond. B Biol. Sci.* 270, S206–S208. <https://doi.org/10.1098/rsbl.2003.0050>.
- Kelley, P.H., 1982. The effect of predation on Miocene mollusc populations of the Chesapeake Group. *Fla. Bur. Geol. Spec. Publ.* 25, 35–48.
- Kelley, P.H., 1988. Predation by Miocene gastropods of the Chesapeake Group: stereotyped and predictable. *PALAIOS* 3, 436–448. <https://doi.org/10.2307/3514789>.
- Kelley, P.H., 1989. Evolutionary trends within bivalve prey of Chesapeake Group naticid gastropods. *Hist. Biol.* 2, 139–156. <https://doi.org/10.1080/08912968909386497>.
- Kelley, P.H., 1991a. Apparent cannibalism by Chesapeake Group naticid gastropods: a predictable result of selective predation. *J. Paleontol.* 65, 75–79. <https://doi.org/10.1017/S0022336000020229>.
- Kelley, P.H., 1991b. The effect of predation intensity on rate of evolution of five Miocene bivalves. *Hist. Biol.* 5, 65–78. <https://doi.org/10.1080/10292389109380388>.
- Kelley, P.H., 2008. Role of bioerosion in taphonomy: effect of predatory drillholes on preservation of mollusc shells. In: Wissak, M., Tapanila, L. (Eds.), *Current Developments in Bioerosion*. Springer, Berlin, Heidelberg, pp. 451–470. https://doi.org/10.1007/978-3-540-77598-0_23.
- Kelley, P.H., Hansen, T.A., 1993. Evolution of the naticid gastropod predator-prey system: an evaluation of the hypothesis of escalation. *PALAIOS* 8, 358–375. <https://doi.org/10.2307/3515266>.
- Kelley, P.H., Hansen, T.A., 1996. Recovery of the naticid gastropod predator-prey system from the Cretaceous-Tertiary and Eocene-Oligocene extinctions. *Geol. Soc. Lond. Spec. Publ.* 102, 373–386. <https://doi.org/10.1144/GSL.SP.1996.001.01.27>.
- Kelley, P.H., Hansen, T.A., 2001. The role of ecological interactions in the evolution of naticid gastropods and their molluscan prey. In: Allmon, W.D., Bottjer, D.J. (Eds.), *Evolutionary Paleocology: The Ecological Context of Macroevolutionary Change*. Columbia University Press, New York, Chichester, pp. 149–170.
- Kelley, P.H., Hansen, T.A., 2003. The fossil record of drilling predation on bivalves and gastropods. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 113–139. https://doi.org/10.1007/978-1-4615-0161-9_6.
- Kelley, P.H., Hansen, T.A., 2006. Comparisons of class- and lower taxon-level patterns in naticid gastropod predation, Cretaceous to Pleistocene of the U.S. Coastal Plain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 236, 302–320. <https://doi.org/10.1016/j.palaeo.2005.11.012>.
- Kelley, P.H., Hansen, T.A., 2007. Latitudinal patterns in naticid gastropod predation along the east coast of the United States: a modern baseline for interpreting temporal patterns in the fossil record. *SEPM Spec. Publ.* 88, 287–299. <https://doi.org/10.2110/pec.07.88.0287>.
- Kelley, P.H., Hansen, T.A., Graham, S.E., Huntoon, A.G., 2001. Temporal patterns in the efficiency of naticid gastropod predators during the Cretaceous and Cenozoic of the United States Coastal Plain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 166, 165–176. [https://doi.org/10.1016/S0031-0182\(00\)00207-8](https://doi.org/10.1016/S0031-0182(00)00207-8).
- Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), 2003. *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow. <https://doi.org/10.1007/978-1-4615-0161-9>.
- Kerr, J.P., Kelley, P.H., 2015. Assessing the influence of escalation during the Mesozoic Marine Revolution: Shell breakage and adaptation against enemies in Mesozoic ammonites. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 440, 632–646. <https://doi.org/10.1016/j.palaeo.2015.08.047>.
- Keupp, H., 1991. Bißmarken oder postmortale Implisionsstrukturen. *Fossilien* 5, 275–280.
- Keupp, H., Hoffmann, R., Stevens, K., Albersdörfer, R., 2016. Key innovations in Mesozoic ammonoids: the multicuspidate radula and the calcified aptychus. *Palaeontology* 59, 775–791. <https://doi.org/10.1111/pala.12254>.
- Keyes, C.R., 1888. On the attachment of *Platyceras* to palaeocrinoids, and its effects in modifying the form of the shell. *Proc. Am. Philos. Soc.* 25, 231–243.
- Kidwell, S.M., 2007. Discordance between living and death assemblages as evidence for anthropogenic ecological change. *Proc. Natl. Acad. Sci.* 104, 17701–17706. <https://doi.org/10.1073/pnas.0707194104>.
- Kidwell, S.M., 2013. Time-averaging and fidelity of modern death assemblages: building a taphonomic foundation for conservation palaeobiology. *Palaeontology* 56, 487–522. <https://doi.org/10.1111/pala.12042>.
- Kidwell, S.M., Baumiller, T.K., 1990. Experimental disintegration of regular echinoids: Roles of temperature, oxygen, and decay thresholds. *Paleobiology* 16, 247–271. <https://doi.org/10.1017/S0094837300009982>.
- Kidwell, S.M., Rothfus, T.A., 2010. The living, the dead, and the expected dead: Variation in life span yields little bias of proportional abundances in bivalve death assemblages. *Paleobiology* 36, 615–640. <https://doi.org/10.1666/09004.1>.
- Kidwell, S.M., Tomašových, A., 2013. Implications of time-averaged death assemblages for ecology and conservation biology. *Annu. Rev. Ecol. Syst.* 44, 539–563. <https://doi.org/10.1146/annurev-ecolsys-110512-135838>.
- Kiel, S., 2010. On the potential generality of depth-related ecologic structure in cold-seep communities: evidence from Cenozoic and Mesozoic examples. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 295, 245–257. <https://doi.org/10.1016/j.palaeo.2010.05.042>.
- Kiel, S., Goedert, J.L., Kahl, W.-A., Rouse, G.W., 2010. Fossil traces of the bone-eating worm *Osedax* in early Oligocene whale bones. *Proc. Natl. Acad. Sci.* 107, 8656–8659. <https://doi.org/10.1073/pnas.1002014107>.
- Kiel, S., Amano, K., Jenkins, R.G., 2016. Predation scar frequencies in chemosymbiotic bivalves at an Oligocene seep deposit and their potential relation to inferred sulfide tolerances. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 453, 139–145. <https://doi.org/10.1016/j.palaeo.2016.04.026>.
- Kier, P.M., 1981. A bored Cretaceous echinoid. *J. Paleontol.* 55, 656–659.
- Kiessling, W., 2009. Geologic and biologic controls on the evolution of reefs. *Annu. Rev. Ecol. Syst.* 40, 173–192. <https://doi.org/10.1146/annurev-ecolsys.110308.120251>.
- Kiessling, W., Simpson, C., 2011. On the potential for ocean acidification to be a general cause of ancient reef crises. *Glob. Change Biol.* 17, 56–67. <https://doi.org/10.1111/j.1365-2486.2010.02204.x>.
- Kimmig, J., Pratt, B.R., 2018. Coprolites in the Ravens Throat River Lagerstätte of northwestern Canada: implications for the Middle Cambrian food web. *PALAIOS* 33, 125–140. <https://doi.org/10.2110/palo.2017.038>.
- Kingsley-Smith, P.R., Richardson, C.A., Seed, R., 2003. Stereotypic and size-selective predation in *Polinices pulchellus* (Gastropoda: Naticidae) Risso 1826. *J. Exp. Mar. Biol. Ecol.* 295, 173–190. [https://doi.org/10.1016/S0022-0981\(03\)00294-6](https://doi.org/10.1016/S0022-0981(03)00294-6).
- Kislalioglu, M., Gibson, R.N., 1976. Prey ‘handling time’ and its importance in food selection by the 15-spined stickleback, *Spinachia spinachia* (L.). *J. Exp. Mar. Biol. Ecol.* 25, 151–158. [https://doi.org/10.1016/0022-0981\(76\)90016-2](https://doi.org/10.1016/0022-0981(76)90016-2).
- Kitchell, J.A., 1986. The evolution of predator-prey behavior: Naticid gastropods and their molluscan prey. In: Nitecki, M., Kitchell, J.A. (Eds.), *Evolution of Animal Behavior: Paleontological and Field Approaches*. Oxford University Press, Oxford, pp. 88–110.
- Kitchell, J.A., Boggs, C.H., Kitchell, J.F., Rice, J.A., 1981. Prey selection by naticid

- gastropods: experimental tests and application to the fossil record. *Paleobiology* 7, 533–552. <https://doi.org/10.1017/S0094837300025574>.
- Kitchell, J.A., Boggs, C.H., Rice, J.A., Kitchell, J.F., Hoffman, A., Martinell, J., 1986. Anomalies in naticid predatory behavior: a critique and experimental observations. *Malacologia* 27, 291–298.
- Klompmaker, A.A., 2009. Taphonomic bias on drill-hole predation intensities and paleoecology of Pliocene mollusks from Langenboom (Mill), The Netherlands. *PALAIOS* 24, 772–779. <https://doi.org/10.2110/palo.2009.p09-023r>.
- Klompmaker, A.A., 2011. Drilling and crushing predation on scaphopods from the Miocene of the Netherlands. *Lethaia* 44, 429–439. <https://doi.org/10.1111/j.1502-3931.2010.00254.x>.
- Klompmaker, A.A., 2012. Drill hole predation on fossil serpulid polychaetes, with new data from the Pliocene of the Netherlands. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 321–322, 113–120. <https://doi.org/10.1016/j.palaeo.2012.01.024>.
- Klompmaker, A.A., Fraaije, R.H.B., 2012. Animal behavior frozen in time: gregarious behavior of Early Jurassic lobsters within an ammonoid body chamber. *PLoS One* 7, e31893. <https://doi.org/10.1371/journal.pone.0031893>.
- Klompmaker, A.A., Kelley, P.H., 2015. Shell ornamentation as a likely exaptation: evidence from predatory drilling on Cenozoic bivalves. *Paleobiology* 41, 187–201. <https://doi.org/10.1017/pab.2014.12>.
- Klompmaker, A.A., Waljaard, N.A., Fraaije, R.H.B., 2009. Ventral bite marks in Mesozoic ammonoids. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 280, 245–257. <https://doi.org/10.1016/j.palaeo.2009.06.013>.
- Klompmaker, A.A., Karasawa, H., Portell, R.W., Fraaije, R.H.B., Ando, Y., 2013. An overview of predation evidence found on fossil decapod crustaceans with new examples of drill holes attributed to gastropods and octopods. *PALAIOS* 28, 599–613. <https://doi.org/10.2110/palo.2013.p13-026r>.
- Klompmaker, A.A., Portell, R.W., Karasawa, H., 2014. First fossil evidence of a drill hole attributed to an octopod in a barnacle. *Lethaia* 47, 309–312. <https://doi.org/10.1111/let.12072>.
- Klompmaker, A.A., Portell, R.W., Lad, S.E., Kowalewski, M., 2015. The fossil record of drilling predation on barnacles. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 426, 95–111. <https://doi.org/10.1016/j.palaeo.2015.02.035>.
- Klompmaker, A.A., Nützel, A., Kaim, A., 2016a. Drill hole convergence and a quantitative analysis of drill holes in mollusks and brachiopods from the Triassic of Italy and Poland. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 457, 342–359. <https://doi.org/10.1016/j.palaeo.2016.06.017>.
- Klompmaker, A.A., Portell, R.W., Van der Meij, S.E.T., 2016b. Trace fossil evidence of coral-inhabiting crabs (Cryptochiridae) and its implications for growth and paleobiogeography. *Sci. Rep.* 6, 23443. <https://doi.org/10.1038/srep23443>.
- Klompmaker, A.A., Kowalewski, M., Huntley, J.W., Finnegan, S., 2017. Increase in predator-prey size ratios throughout the Phanerozoic history of marine ecosystems. *Science* 356, 1178–1180. <https://doi.org/10.1126/science.aam7468>.
- Klompmaker, A.A., Nyborg, T.G., Brezina, J., Ando, Y., 2018. Crustaceans in cold seep ecosystems: Fossil record, geographic distribution, taxonomic composition, and biology. *Paleorxiv Prepr.* <https://doi.org/10.31233/osf.io/tws6m>.
- Kluessendorf, J., 1983. Observations on the commensalism of Silurian platyceratid gastropods and stalked echinoderms. *Wis. Acad. Sci. Arts Lett.* 71, 48–55.
- Klug, C., 2007. Sublethal injuries in Early Devonian cephalopod shells from Morocco. *Acta Palaeontol. Pol.* 52, 749–759.
- Klug, C., Vallon, L.H., 2018. Regurgitated ammonoid remains from the latest Devonian of Morocco. *Swiss J. Palaeontol.* <https://doi.org/10.1007/s13358-018-0171-z>.
- Knoll, A.H., Bambach, R.K., 2000. Directionality in the history of life: Diffusion from the left wall or repeated scaling of the right? *Paleobiology* 26, 1–14. [https://doi.org/10.1666/0094-8373\(2000\)26\[1:DITHOL\]2.0.CO;2](https://doi.org/10.1666/0094-8373(2000)26[1:DITHOL]2.0.CO;2).
- Kočí, T., Veselská, M.K., Gale, A.S., Jagt, J.W.M., Skupien, P., 2015. Late Jurassic–Early Cretaceous stalked barnacles (Cirripedia, genus *Eolepas* Withers, 1928) from Štramberk, Moravia (Czech Republic). *Neues Jahrb. für Geol. Paläontol. Abh.* 275, 233–247.
- Kohn, A.J., 1999. Anti-predator defences of shelled gastropods. In: Savazzi, E. (Ed.), *Functional Morphology of the Invertebrate Skeleton*. John Wiley & Sons, Chichester, pp. 169–181.
- Kohn, A.J., Arua, I., 1999. An Early Pleistocene molluscan assemblage from Fiji: gastropod faunal composition, paleoecology and biogeography. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 146, 99–145. [https://doi.org/10.1016/S0031-0182\(98\)00135-7](https://doi.org/10.1016/S0031-0182(98)00135-7).
- Kojumdjieva, E., 1974. Les gasteropodes perçeurs et leurs victimes du Miocene de Bulgarie du nord-ouest. *Bulg. Acad. Sci. Bull. Geol. Inst. Paleontol.* 25, 5–24.
- Kong, D.-Y., Lee, M.-H., Lee, S.-J., 2015. Traces (ichnospecies *Oichnus paraboloides*) of predatory gastropods on bivalve shells from the Seogwipo Formation, Jeju-do, Korea. *J. Asia-Pac. Biodivers.* 8, 330–336. <https://doi.org/10.1016/j.japb.2015.10.013>.
- Kong, D.-Y., Lee, M.-H., Park, C.H., Lee, S.-J., 2017. Boreholes on three bivalve species found on the sand beach at Sagot Cape, Baengnyeongdo, Korea. *J. Asia-Pac. Biodivers.* 10, 441–447. <https://doi.org/10.1016/j.japb.2017.09.004>.
- Konishi, T., Brinkman, D., Massare, J.A., Caldwell, M.W., 2011. New exceptional specimens of *Prognathodon overtoni* (Squamata, Mosasauridae) from the upper Campanian of Alberta, Canada, and the systematics and ecology of the genus. *J. Vertebr. Paleontol.* 31, 1026–1046. <https://doi.org/10.1080/02724634.2011.601714>.
- Kontrovitz, M., 1975. A study of the differential transportation of ostracodes. *J. Paleontol.* 49, 937–941.
- Kontrovitz, M., Snyder, S.W., 1981. Reliability of microfossil assemblages as paleoenvironmental indicators. *Trans. Gulf Coast Assoc. Geol. Soc.* 31, 323–324.
- Kontrovitz, M., Snyder, S.W., Brown, R.J., 1978. A flume study of the movement of Foraminifera tests. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 23, 141–150. [https://doi.org/10.1016/0031-0182\(78\)90086-X](https://doi.org/10.1016/0031-0182(78)90086-X).
- Kordas, R.L., Harley, C.D.G., O'Connor, M.I., 2011. Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. *J. Exp. Mar. Biol. Ecol.* 400, 218–226. <https://doi.org/10.1016/j.jembe.2011.02.029>.
- Kornicker, L.S., Armstrong, N., 1959. Mobility of partially submerged shells. *Inst. Mar. Sci. Publ.* 6, 171–185.
- Kornicker, L.S., Wise, C.D., Wise, J.M., 1963. Factors affecting the distribution of opposing mollusk valves. *J. Sediment. Res.* 33, 703–712. <https://doi.org/10.1306/74D70F01-2B21-11D7-8648000102C1865D>.
- Kosloski, M., 2011. Recognizing biotic breakage of the hard clam, *Mercenaria mercenaria* caused by the stone crab, *Menippe mercenaria*: an experimental taphonomic approach. *J. Exp. Mar. Biol. Ecol.* 396, 115–121. <https://doi.org/10.1016/j.jembe.2010.10.010>.
- Kosnik, M.A., 2005. Changes in Late Cretaceous–early Tertiary benthic marine assemblages: analyses from the North American coastal plain shallow shelf. *Paleobiology* 31, 459–479. [https://doi.org/10.1666/0094-8373\(2005\)031\[0459:CILCTB\]2.0.CO;2](https://doi.org/10.1666/0094-8373(2005)031[0459:CILCTB]2.0.CO;2).
- Kosuge, S., 1971. Notes on *Thyca crystallina* (Gould). *Chiribotan* 6, 123–125.
- Kosuge, S., Hayashi, S., 1967. Notes on the feeding habits of *Capulus dilatatus*. *Sci. Rep. Yokosuka City Mus.* 13, 45–54.
- Kowalewski, M., 1990. A hermeneutic analysis of the shell-drilling gastropod predation on mollusks in the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Pol.* 40, 183–213.
- Kowalewski, M., 2002. The fossil record of predation: an overview of analytical methods. *Paleontol. Soc. Pap.* 8, 3–42. <https://doi.org/10.1017/S1089332600001030>.
- Kowalewski, M., 2004. Drill holes produced by the predatory gastropod *Nucella lamellosa* (Muricidae): Palaeobiological and ecological implications. *J. Molluscan Stud.* 70, 359–370. <https://doi.org/10.1093/mollus/70.4.359>.
- Kowalewski, M., Hoffmeister, A.P., 2003. Sieves and fossils: Effects of mesh size on paleontological patterns. *PALAIOS* 18, 460–469. [https://doi.org/10.1669/0883-1351\(2003\)018<0460:SAFEOM>2.0.CO;2](https://doi.org/10.1669/0883-1351(2003)018<0460:SAFEOM>2.0.CO;2).
- Kowalewski, M., Kelley, P.H., 2002. The Fossil Record of Predation, Paleontological Society Special Papers 8. The Paleontological Society, New Haven.
- Kowalewski, M., Nebelsick, J.H., 2003. Predation on recent and fossil echinoids. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 279–302. https://doi.org/10.1007/978-1-4615-0161-9_12.
- Kowalewski, M., Dulai, A., Fürsich, F.T., 1998. A fossil record full of holes: the Phanerozoic history of drilling predation. *Geology* 26, 1091–1094. [https://doi.org/10.1130/0091-7613\(1998\)026<1091:AFRFOH>2.3.CO;2](https://doi.org/10.1130/0091-7613(1998)026<1091:AFRFOH>2.3.CO;2).
- Kowalewski, M., Simões, M.G., Torello, F.F., Mello, L.H.C., Ghilardi, R.P., 2000. Drill holes in shells of Permian benthic invertebrates. *J. Paleontol.* 74, 532–543. <https://doi.org/10.1017/S0022336000031796>.
- Kowalewski, M., Hoffmeister, A.P., Baumiller, T.K., Bambach, R.K., 2005. Secondary evolutionary escalation between brachiopods and enemies of other prey. *Science* 308, 1774–1777. <https://doi.org/10.1126/science.1113408>.
- Krantz, G.E., Chamberlin, J.V., 1978. Blue crab predation on cultchless oyster spat. *Proc. Natl. Shellfish. Assoc.* 68, 38–41.
- Kroeker, K.J., Kordas, R.L., Crim, R., Hendriks, I.E., Ramajo, L., Singh, G.S., Duarte, C.M., Gattuso, J.-P., 2013. Impacts of ocean acidification on marine organisms: Quantifying sensitivities and interaction with warming. *Glob. Change Biol.* 19, 1884–1896. <https://doi.org/10.1111/gcb.12179>.
- Kroeker, K.J., Sanford, E., Jellison, B.M., Gaylord, B., 2014. Predicting the effects of ocean acidification on predator-prey interactions: a conceptual framework based on coastal molluscs. *Biol. Bull.* 226, 211–222. <https://doi.org/10.1086/BBLv226n3p211>.
- Kroeker, K.J., Sanford, E., Rose, J.M., Blanchette, C.A., Chan, F., Chavez, F.P., Gaylord, B., Helmuth, B., Hill, T.M., Hofmann, G.E., McManus, M.A., Menge, B.A., Nielsen, K.J., Raimond, P.T., Russell, A.D., Washburn, L., 2016. Interacting environmental mosaics drive geographic variation in mussel performance and predation vulnerability. *Ecol. Lett.* 19, 771–779. <https://doi.org/10.1111/ele.12613>.
- Kröger, B., 2002. Antipredatory traits of the ammonoid shell - indications from Jurassic ammonoids with sublethal injuries. *Paläontol. Z.* 76, 223–234. <https://doi.org/10.1007/BF02989859>.
- Kröger, B., 2004. Large shell injuries in Middle Ordovician Orthocerida (Nautiloidea, Cephalopoda). *GFF* 126, 311–316. <https://doi.org/10.1080/11035890401263311>.
- Kröger, B., 2011. Size matters - Analysis of shell repair scars in endocerid cephalopods. *Foss. Rec.* 14, 109–118. <https://doi.org/10.5194/fr-14-109-2011>.
- Kröger, B., Vinther, J., Fuchs, D., 2011. Cephalopod origin and evolution: a congruent picture emerging from fossils, development and molecules. *BioEssays* 33, 602–613. <https://doi.org/10.1002/bies.201100001>.
- Kropp, R.K., 1992. Repaired shell damage among soft-bottom mollusks on the continental shelf and upper slope north of Point Conception, California. *The Veliger* 35, 36–51.
- Kubicka, A.M., Rosin, Z.M., Tryjanowski, P., Nelson, E., 2017. A systematic review of animal predation creating pierced shells: implications for the archaeological record of the Old World. *PeerJ* 5, e2903. <https://doi.org/10.7717/peerj.2903>.
- LaBarbera, M., 1977. Brachiopod orientation to water movement. I. Theory, laboratory behavior, and field orientations. *Paleobiology* 3, 270–287. <https://doi.org/10.1017/S0094837300005376>.
- Lambert, W.J., 1991. Coexistence of hydroid eating nudibranchs: do feeding biology and habitat use matter? *Biol. Bull.* 181, 248–260.
- Landman, N.H., Klofak, S.M., 2012. Anatomy of a concretion: Life, death, and burial in the Western Interior Seaway. *PALAIOS* 27, 671–692. <https://doi.org/10.2110/palo.2011.p11-105r>.
- Landman, N.H., Waage, K.M., 1986. Shell abnormalities in scaphitid ammonites. *Lethaia* 19, 211–224. <https://doi.org/10.1111/j.1502-3931.1986.tb00734.x>.
- Landman, N.H., Fraaije, R.H.B., Klofak, S.M., Larson, N.L., Bishop, G.A., Kruta, I., 2014. Inquinism of a baculite by a dymenoid crab from the Upper Cretaceous of South Dakota. *Am. Mus. Novit.* 3818, 1–16. <https://doi.org/10.1206/3818.1>.

- Langerhans, R.B., 2007. Evolutionary consequences of predation: avoidance, escape, reproduction, and diversification. In: Elewa, A.M.T. (Ed.), *Predation in Organisms*. Springer, Berlin, Heidelberg, pp. 177–220. https://doi.org/10.1007/978-3-540-46046-6_10.
- Larcombe, M.F., 1971. *The Ecology, Population Dynamics and Energetics of some Soft Shore Molluscs* (Dissertation). University of Auckland, Auckland, New Zealand.
- Larsson, C., 1979. Silurian tentaculitids from Gotland and Scania. *Foss. Strata* 1–180.
- Laserer, C.F., 1957. A new classification of the Australian Marginellidae (Mollusca), with a review of species from the Solanderian and Dampierian zoogeographical provinces. *Mar. Freshw. Res.* 8, 274–311.
- Laws, H.M., Laws, D.F., 1972. The escape response of *Donacilla angusta* Reeve (Mollusca: Bivalvia) in the presence of a naticid predator. *The Veliger* 14, 289–290.
- Lebedev, O.A., Mark-Kurik, E., Karatjütë-Talimaa, V.N., Lukševičs, E., Ivanov, A., 2009. Bite marks as evidence of predation in early vertebrates. *Acta Zool.* 90, 344–356. <https://doi.org/10.1111/j.1463-6395.2008.00344.x>.
- Leduc, A.O.H.C., Munday, P.L., Brown, G.E., Ferrari, M.C.O., 2013. Effects of acidification on olfactory-mediated behaviour in freshwater and marine ecosystems: a synthesis. *Philos. Trans. R. Soc. B Biol. Sci.* 368, 20120447. <https://doi.org/10.1098/rstb.2012.0447>.
- Lehman, V., 1971. Jaws, radula, and crop of *Amniceras* (Ammonoidea). *Palaeontology* 14, 338–341.
- Lehmann, W.M., 1951. Anomalien und Regenerationserscheinungen an paläozoischen Asterozoen. *Neues Jahrb. für Geol. Paläontol. Abh.* 93, 401–416.
- Lehmann, U., 1975. Über Nahrung und Ernährungsweise von Ammoniten. *Paläontol. Z.* 49, 187–195. <https://doi.org/10.1007/BF02987657>.
- Lehmann, U., Kulicki, C., 1990. Double function of apychi (Ammonoidea) as jaw elements and opercula. *Lethaia* 23, 325–331. <https://doi.org/10.1111/j.1502-3931.1990.tb01365.x>.
- Leibold, M.A., 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.* 134, 922–949. <https://doi.org/10.1086/285022>.
- Leighton, L.R., 2001. New example of Devonian predatory boreholes and the influence of brachiopod spines on predator success. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 165, 53–69. [https://doi.org/10.1016/S0031-0182\(00\)00153-X](https://doi.org/10.1016/S0031-0182(00)00153-X).
- Leighton, L.R., 2002. Inferring predation intensity in the marine fossil record. *Paleobiology* 28, 328–342. [https://doi.org/10.1666/0094-8373\(2002\)028<0328:IPITM>2.0.CO;2](https://doi.org/10.1666/0094-8373(2002)028<0328:IPITM>2.0.CO;2).
- Leighton, L.R., 2003a. Predation on brachiopods. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 215–237. https://doi.org/10.1007/978-1-4615-0161-9_9.
- Leighton, L.R., 2003b. Morphological response of prey to drilling predation in the Middle Devonian. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 201, 221–234. [https://doi.org/10.1016/S0031-0182\(03\)00627-8](https://doi.org/10.1016/S0031-0182(03)00627-8).
- Leighton, L.R., Webb, A.E., Sawyer, J.A., 2013. Ecological effects of the Paleozoic-Modern faunal transition: comparing predation on Paleozoic brachiopods and molluscs. *Geology* 41, 275–278. <https://doi.org/10.1130/G33750.1>.
- Leighton, L.R., Chojnacki, N.C., Stafford, E.S., Tyler, C.L., Schneider, C.L., 2016. Categorization of shell fragments provides a proxy for environmental energy and predation intensity. *J. Geol. Soc.* 173, 711–715. <https://doi.org/10.1144/jgs2015-086>.
- Leonard-Pingel, J.S., Jackson, J.B.C., 2013. Drilling intensity varies among Neogene tropical American Bivalvia in relation to shell form and life habit. *Bull. Mar. Sci.* 89, 905–919. <https://doi.org/10.5343/bms.2012.1058>.
- Leonard-Pingel, J.S., Jackson, J.B.C., 2016. Drilling predation increased in response to changing environments in the Caribbean Neogene. *Paleobiology* 42, 394–409. <https://doi.org/10.1017/pab.2016.2>.
- Lescinsky, H.L., Benninger, L., 1994. Pseudo-borings and predator traces: Artifacts of pressure-dissolution in fossiliferous shales. *PALAIOS* 9, 599–604. <https://doi.org/10.2307/3515130>.
- Lever, J., 1958. Quantitative beach research. I. The “left-right-phenomenon”: sorting of lamellibranch valves on sandy beaches. *Basteria* 22, 21–51.
- Lever, J., Thijssen, R., 1968. Sorting phenomena during the transport of shell valves on sandy beaches studied with the use of artificial valves. In: Fretter, V. (Ed.), *Studies in the Structure, Physiology, and Ecology of Molluscs*, Symposia of the Zoological Society of London, pp. 259–271.
- Lever, J., Kessler, A., Van Overbeek, A.P., Thijssen, R., 1961. Quantitative beach research II, the “hole effect”: a second mode of sorting of lamellibranch valves on sandy beaches. *Neth. J. Sea Res.* 1, 339–353.
- Levin, L.A., Ekau, W., Gooday, A.J., Jorissen, F., Middelburg, J.J., Naqvi, S.W.A., Neira, C., Rabalais, N.N., Zhang, J., 2009. Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences* 6, 2063–2098. <https://doi.org/10.5194/bg-6-2063-2009>.
- Levitan, D.R., Genovese, S.J., 1989. Substratum-dependent predator-prey dynamics: Patch reefs as refuges from gastropod predation. *J. Exp. Mar. Biol. Ecol.* 130, 111–118. [https://doi.org/10.1016/0022-0981\(89\)90198-6](https://doi.org/10.1016/0022-0981(89)90198-6).
- Lewy, Z., Samtleben, C., 1979. Functional morphology and palaeontological significance of the conchiolin layers in corbulid pelecypods. *Lethaia* 12, 341–351. <https://doi.org/10.1111/j.1502-3931.1979.tb01019.x>.
- Li, R.-Y., Young, H.R., Zhan, R.-B., 2011. Drilling predation on scaphopods and other molluscs from the Upper Cretaceous of Manitoba, Canada. *Palaeoworld* 20, 296–307. <https://doi.org/10.1016/j.palwor.2011.04.001>.
- Lima, S.L., Bednekoff, P.A., 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* 153, 649–659. <https://doi.org/10.1086/303202>.
- Lindström, A., Peel, J.S., 2010. Shell repair and shell form in Jurassic pleurotomarioid gastropods from England. *Bull. Geosci.* 85, 541–550. <https://doi.org/10.3140/bull.geosci.1205>.
- Long, J.A., 1995. *The Rise of Fishes: 500 Million Years of Evolution*. The John Hopkins University Press, Baltimore.
- Long, W.C., Brylawski, B.J., Seitz, R.D., 2008. Behavioral effects of low dissolved oxygen on the bivalve *Macoma balthica*. *J. Exp. Mar. Biol. Ecol.* 359, 34–39. <https://doi.org/10.1016/j.jembe.2008.02.013>.
- Lord, J., Whitlatch, R., 2013. Impact of temperature and prey shell thickness on feeding of the oyster drill *Urosalpinx cinerea* Say. *J. Exp. Mar. Biol. Ecol.* 448, 321–326. <https://doi.org/10.1016/j.jembe.2013.08.006>.
- Loydell, D.K., Zalasiewicz, J., Cave, R., 1998. Predation on graptoloids: new evidence from the Silurian of Wales. *Palaeontology* 41, 423–427.
- Ludvigsen, R., 1977. Rapid repair of traumatic injury by an Ordovician trilobite. *Lethaia* 10, 205–207. <https://doi.org/10.1111/j.1502-3931.1977.tb00613.x>.
- Lund, R., Lund, W., 1984. New genera and species of coelacanth from the Bear Gulch Limestone (Lower Carboniferous) of Montana (U.S.A.). *Geobios* 17, 237–244. [https://doi.org/10.1016/S0016-6995\(84\)80145-X](https://doi.org/10.1016/S0016-6995(84)80145-X).
- Lund, R., Lund, W.L., 1985. Coelacanths from the Bear Gulch Limestone (Namurian) of Montana and the evolution of the Coelacanthiformes. *Bull. Carnegie Mus. Nat. Hist.* 25, 1–74.
- MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. *Am. Nat.* 100, 603–609. <https://doi.org/10.1086/282454>.
- Macurda, D.B., 1965. The functional morphology and stratigraphic distribution of the Mississippian blastoid genus *Orophocrinus*. *J. Paleontol.* 39, 1045–1096.
- Maddocks, R.F., 1988. One hundred million years of predation on ostracodes: The fossil record in Texas. In: Hanai, T., Ikeya, N., Ishizaki, K. (Eds.), *Evolutionary Biology of Ostracods*. Developments in Palaeontology and Stratigraphy. Elsevier, Amsterdam, pp. 637–657.
- Maeda, H., Seilacher, A., 1996. Ammonoid taphonomy. In: Landman, N.H., Tanabe, K., Davis, R.A. (Eds.), *Ammonoid Paleobiology, Topics in Geobiology*. Springer, New York, pp. 543–578.
- Maisey, J.G., 1994. Predator-prey relationships and trophic level reconstruction in a fossil fish community. *Environ. Biol. Fish* 40, 1–22. <https://doi.org/10.1007/BF00002179>.
- Malinky, J.M., Skovsted, C.B., 2004. Hyoliths and small shelly fossils from the Lower Cambrian of north-east Greenland. *Acta Palaeontol. Pol.* 49, 551–578.
- Mallick, S., Bardhan, S., Paul, S., Mukherjee, S., Das, S.S., 2013. Intense naticid drilling predation on turritelline gastropods from below the K-T boundary at Rajahmundry, India. *PALAIOS* 28, 683–696. <https://doi.org/10.2110/palo.2013.p13-007r>.
- Mallick, S., Bardhan, S., Das, S.S., Paul, S., Goswami, P., 2014. Naticid drilling predation on gastropod assemblages across the K-T boundary in Rajahmundry, India: New evidence for escalation hypothesis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 411, 216–228. <https://doi.org/10.1016/j.palaeo.2014.07.001>.
- Mallick, S., Bardhan, S., Paul, S., Goswami, P., Das, S.S., 2017. Record of naticid predation on scaphopods (Mollusca) from the latest Mastrichtian of Rajahmundry, India. *Ichnos* 24, 37–50. <https://doi.org/10.1080/10420940.2015.1126584>.
- Malumíán, N., López Cabrera, M.L., Nández, C., Olivero, E.B., 2007. Bioerosion patterns in Cretaceous-Cenozoic benthic foraminiferal tests from Patagonia and Tierra del Fuego Island, Argentina. In: Buatois, L.A., Mangano, G., Genise, J.F., Melchor, R.N. (Eds.), *Sediment-Organism Interactions; A Multifaceted Ichnology*, Special Publication - Society for Sedimentary Geology, pp. 301–308.
- Manzi, J.J., 1970. Combined effects of salinity and temperature on the feeding, reproductive, and survival rates of *Eupleura caudata* (Say) and *Urosalpinx cinerea* (Say) (Prosobranchia: Muricidae). *Biol. Bull.* 138, 35–46.
- Mapes, R.H., Chaffin, D.T., 2003. Predation on cephalopods: A general overview with a case study from the Upper Carboniferous of Texas. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 177–213. https://doi.org/10.1007/978-1-4615-0161-9_8.
- Mapes, R.H., Hansen, M.C., 1984. Pennsylvanian shark-cephalopod predation: a case study. *Lethaia* 17, 175–183. <https://doi.org/10.1111/j.1502-3931.1984.tb01613.x>.
- Mapes, R.H., Fahrner, T.R., Babcock, L.E., 1989. Sublethal and lethal injuries of Pennsylvanian conulariids from Oklahoma. *J. Paleontol.* 63, 34–37. <https://doi.org/10.1017/S0022336000040920>.
- Mapes, R.H., Sims, M.S., Boardman, D.R., 1995. Predation on the Pennsylvanian ammonoid *Gonioloboceras* and its implications for allochthonous vs. autochthonous accumulations of *Goniatites* and other ammonoids. *J. Paleontol.* 69, 441–446. <https://doi.org/10.1017/S0022336000034843>.
- Mapes, R.H., Landman, N.H., Cochran, K., Goiran, C., Richer de Forges, B., Renfro, A., 2010. Early taphonomy and significance of naturally submerged *Nautilus* shells from the New Caledonia region. *PALAIOS* 25, 597–610. <https://doi.org/10.2110/palo.2009.p09-109r>.
- Martill, D.M., 1990. Predation on *Kosmoceras* by semionotid fish in the Middle Jurassic Lower Oxford Clay of England. *Palaeontology* 33, 739–742.
- Martin, J.E., Björk, P.R., 1987. Gastric residues associated with the mosasaur *Tylosaurus* from the Late Cretaceous (Campanian) Pierre Shale, South Dakota. *Dakoterra* 3, 68–70.
- Martin, L.D., Rothschild, B.M., 1989. Paleopathology and diving mosasaurs. *Am. Sci.* 77, 460–467.
- Martinell, J., Domènech, R., Aymar, J., Kowalewski, M., 2010. Confamilial predation in Pliocene naticid gastropods from southern France: utility of preexisting collections in quantitative paleoecology. *PALAIOS* 25, 221–228. <https://doi.org/10.2110/palo.2009.p09-124r>.
- Martinell, J., Kowalewski, M., Domènech, R., 2012. Drilling predation on serpulid polychaetes (*Ditrupa arietina*) from the Pliocene of the Cope Basin, Murcia region, southeastern Spain. *PLoS One* 7, e34576. <https://doi.org/10.1371/journal.pone.0034576>.

- Martinelli, J.C., Gordillo, S., Archuby, F., 2013. Muricid drilling predation at high latitudes: Insights from the southernmost Atlantic. *PALAIOS* 28, 33–41. <https://doi.org/10.2110/palo.2012.p12-087r>.
- Martinelli, J.C., Kosnik, M.A., Madin, J.S., 2015. Encounter frequency does not predict predation frequency in tropical dead-shell assemblages. *PALAIOS* 30, 818–826. <https://doi.org/10.2110/palo.2015.039>.
- Martinelli, J.C., Kosnik, M.A., Madin, J.S., 2016. Passive defensive traits are not good predictors of predation for infaunal reef bivalves. *PALAIOS* 31, 607–615. <https://doi.org/10.2110/palo.2016.018>.
- Martin-Kaye, P., 1951. Sorting of lamellibranch valves on beaches in Trinidad, B.W.I. *Geol. Mag.* 88, 432–434. <https://doi.org/10.1017/S0016756800069995>.
- Massare, J.A., 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *J. Vertebr. Paleontol.* 7, 121–137. <https://doi.org/10.1080/02724634.1987.10011647>.
- Massare, J.A., 1988. Swimming capabilities of Mesozoic marine reptiles: implications for method of predation. *Paleobiology* 14, 187–205. <https://doi.org/10.1017/S009483730001191X>.
- Matassa, C.M., Trussell, G.C., 2015. Effects of predation risk across a latitudinal temperature gradient. *Oecologia* 177, 775–784. <https://doi.org/10.1007/s00442-014-3156-7>.
- Matheson, K., Gagnon, P., 2012. Temperature mediates non-competitive foraging in indigenous rock (*Cancer irroratus* Say) and recently introduced green (*Carcinus maenas* L.) crabs from Newfoundland and Labrador. *J. Exp. Mar. Biol. Ecol.* 414–415, 6–18. <https://doi.org/10.1016/j.jembe.2012.01.006>.
- Matsukuma, A., 1977. Notes on *Gemkaimurex varicosa* (Kuroda, 1953) (Prosobranchia: Neogastropoda). *Venus* 36, 81–88.
- Matsukuma, A., 1978. Fossil boreholes made by shell-boring predators or commensals, 1: Boreholes of capulid gastropods. *Venus* 37, 29–45.
- Matsumoto, T., Nihongi, M., 1979. An interesting mode of occurrence of *Polyptychoceras* (Cretaceous heteromorph ammonoid). *Proc. Jpn. Acad. Ser. B* 55, 115–119.
- Maxwell, P.A., 1988. Late Miocene deep-water Mollusca from the Stillwater Mudstone at Greymouth, Westland, New Zealand: Paleocology and systematics. *N. Z. Geol. Surv. Paleontol. Bull.* 55, 1–120.
- McAllister, J., 2003. Predation of fishes in the fossil record. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 303–324. https://doi.org/10.1007/978-1-4615-0161-9_13.
- McClanahan, T.R., 1992. Epibenthic gastropods of the middle Florida Keys: the role of habitat and environmental stress on assemblage composition. *J. Exp. Mar. Biol. Ecol.* 160, 169–190. [https://doi.org/10.1016/0022-0981\(92\)90236-4](https://doi.org/10.1016/0022-0981(92)90236-4).
- McFadden, K.A., Huang, J., Chu, X., Jiang, G., Kaufman, A.J., Zhou, C., Yuan, X., Xiao, S., 2008. Pulsed oxidation and biological evolution in the Ediacaran Doushantuo Formation. *Proc. Natl. Acad. Sci.* 105, 3197–3202. <https://doi.org/10.1073/pnas.0708336105>.
- McHenry, C.R., Cook, A.G., Wroe, S., 2005. Bottom-feeding plesiosaurs. *Science* 310, 75. <https://doi.org/10.1126/science.1117241>.
- McKinney, F.K., Taylor, P.D., Lidgard, S., 2003. Predation on bryozoans and its reflection in the fossil record. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 239–261. https://doi.org/10.1007/978-1-4615-0161-9_10.
- McKittick, M.A., 1987. Experiments on the settling of gastropod and bivalve shells: biostratigraphic implications. In: Flessa, K.W. (Ed.), *Paleoecology and Taphonomy of Recent to Pleistocene Intertidal Deposits, Gulf of California*, The Paleontological Society Special Publications. The Paleontological Society, Phoenix, pp. 150–163.
- McNamara, K.J., 1994. The significance of gastropod predation to patterns of evolution and extinction in Australian Tertiary echinoids. In: David, K., Guille, A., Féral, J.-P., Roux, M. (Eds.), *Echinoderms Through Time*. Balkema, Rotterdam, pp. 785–793.
- Meadows, C.A., Fordyce, R.E., Baumiller, T.K., 2015. Drill holes in the irregular echinoid, *Fibularia*, from the Oligocene of New Zealand. *PALAIOS* 30, 810–817. <https://doi.org/10.2110/palo.2015.043>.
- Menard, H.W., Boucot, A.J., 1951. Experiments on the movement of shells by water. *Am. J. Sci.* 249, 131–151. <https://doi.org/10.2475/ajs.249.2.131>.
- Menge, B.A., 1972. Competition for food between two intertidal starfish species and its effect on body size and feeding. *Ecology* 53, 635–644. <https://doi.org/10.2307/1934777>.
- Merle, D., Garrigues, B., Pointier, J.-P., 2011. *Fossil and Recent Muricidae of the World: Part Muricinae*. ConchBooks, Hackenheim.
- Meyer, D.L., 1985. Evolutionary implications of predation on Recent comatulid crinoids from the Great Barrier Reef. *Paleobiology* 11, 154–164. <https://doi.org/10.1017/S0094837300011477>.
- Meyer, D.L., Macurda, D.B., 1977. Adaptive radiation of the comatulid crinoids. *Paleobiology* 3, 74–82. <https://doi.org/10.1017/S0094837300005121>.
- Micheli, F., Peterson, C.H., Mullineaux, L.S., Fisher, C.R., Mills, S.W., Sancho, G., Johnson, G.A., Lenihan, H.S., 2002. Predation structures communities at deep-sea hydrothermal vents. *Ecol. Monogr.* 72, 365–382. [https://doi.org/10.1890/0012-9615\(2002\)072\[0365:PSCADS\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2002)072[0365:PSCADS]2.0.CO;2).
- Milán, J., Lindow, B.E.K., Lauridsen, B.W., 2011. Bite traces in a turtle carapace fragment from the middle Danian (Lower Paleocene) bryozoan limestone, Faxe, Denmark. *Bull. Geol. Soc. Den.* 59, 61–67.
- Miles, R.S., Westoll, T.S., 1968. IX.—The placoderm fish *Coccosteus cuspidatus* Miller ex Agassiz from the Middle Old Red Sandstone of Scotland. Part I. Descriptive morphology. *Trans. R. Soc. Edinb.* 67, 373–476. <https://doi.org/10.1017/S0080456800024078>.
- Miller, L.P., 2013. The effect of water temperature on drilling and ingestion rates of the dogwhelk *Nuccella lapillus* feeding on *Mytilus edulis* mussels in the laboratory. *Mar. Biol.* 160, 1489–1496. <https://doi.org/10.1007/s00227-013-2202-z>.
- Miller, L.P., Matassa, C.M., Trussell, G.C., 2014. Climate change enhances the negative effects of predation risk on an intermediate consumer. *Glob. Change Biol.* 20, 3834–3844. <https://doi.org/10.1111/gcb.12639>.
- Mironenko, A., 2017. Sublethal injuries on the shells of Jurassic ammonites from Central Russia. In: Rogov, M.A., Zakharov, V.A. (Eds.), *Jurassic Deposits of the Southern Part of the Moscow Syncline and their Fauna*, Transaction of the Geological Institute. GEOS, Moscow, pp. 183–208.
- Moissette, P., Koskeridou, E., Corneé, J.-J., Guillocheau, F., Lecuyer, C., 2007. Spectacular preservation of seagrasses and seagrass-associated communities from the Pliocene of Rhodes, Greece. *PALAIOS* 22, 200–211. <https://doi.org/10.2110/palo.2005.p05-141r>.
- Molinaro, D.J., Collins, B.M.J., Burns, M.E., Stafford, E.S., Leighton, L.R., 2013. Do predatory drill holes influence the transport and deposition of gastropod shells? *Lethaia* 46, 508–517. <https://doi.org/10.1111/let.12030>.
- Molinaro, D.J., Stafford, E.S., Collins, B.M.J., Barclay, K.M., Tyler, C.L., Leighton, L.R., 2014. Peeling out predation intensity in the fossil record: a test of repair scar frequency as a suitable proxy for predation pressure along a modern predation gradient. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 412, 141–147. <https://doi.org/10.1016/j.palaeo.2014.07.033>.
- Mondal, S., Harries, P.J., 2015. Temporal patterns in successful and unsuccessful shell-breaking predatory attack strategies on *Varicorbula* in the Plio-Pleistocene of Florida. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 428, 31–38. <https://doi.org/10.1016/j.palaeo.2015.03.031>.
- Mondal, S., Harries, P.J., Paul, S., Herbert, G.S., 2014. Paleoeological significance of coupling metrics of successful and unsuccessful shell-breaking predation: examples using Neogene bivalve prey. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 399, 89–97. <https://doi.org/10.1016/j.palaeo.2014.02.010>.
- Mondal, S., Goswami, P., Bardhan, S., 2017. Naticid confamilial drilling predation through time. *PALAIOS* 32, 278–287. <https://doi.org/10.2110/palo.2016.050>.
- Morris, S.C., Bengtson, S., 1994. Cambrian predators: possible evidence from boreholes. *J. Paleontol.* 68, 1–23. <https://doi.org/10.1017/S0022366000025567>.
- Morton, B., Britton, J.C., 2002. Holothurian feeding by *Nassarius dorsatus* on a beach in Western Australia. *J. Molluscan Stud.* 68, 187–189. <https://doi.org/10.1093/mollus/68.2.187>.
- Morton, B., Chan, K., 1997. First report of shell boring predation by a member of the Nassariidae (Gastropoda). *J. Molluscan Stud.* 63, 476–478.
- Morton, B., Chan, K., 1999. Hunger rapidly overrides the risk of predation in the subtidal scavenger *Nassarius siquijorensis* (Gastropoda: Nassariidae): an energy budget and a comparison with the intertidal *Nassarius festivus* in Hong Kong. *J. Exp. Mar. Biol. Ecol.* 240, 213–228. [https://doi.org/10.1016/S0022-0981\(99\)00060-X](https://doi.org/10.1016/S0022-0981(99)00060-X).
- Morton, B., Harper, E.M., 2009. Drilling predation upon *Ditrupa arietina* (Polychaeta: Serpulidae) from the mid-Atlantic Azores, Portugal. *Azorean Suppl.* 6, 157–165.
- Morton, B., Peharda, M., Harper, E.M., 2007. Drilling and chipping patterns of bivalve prey predation by *Hexaplex trunculus* (Mollusca: Gastropoda: Muricidae). *J. Mar. Biol. Assoc. U. K.* 87, 933–940. <https://doi.org/10.1017/S0025315407056184>.
- Motani, R., 2008. Combining uniformitarian and historical data to interpret how Earth environment influenced the evolution of Ichthyopterygia. In: Kelley, P.H., Bambach, R.K. (Eds.), *From Evolution to Geobiology: Research Questions Driving Paleontology and the Start of a New Century*. The Paleontological Society Papers, pp. 147–164.
- Muir, L.A., Botting, J.P., 2007. Graptolite faunas and monaxonid demosponges of the *Cyrtograptus lundgreni* event (late Wenlock, Silurian) interval from the Orange district, New South Wales. *Alcheringa* 31, 375–395. <https://doi.org/10.1080/03115510701641148>.
- Müller, A.H., 1969. Über Raubschneckenbefall und Ökologie fossiler Ditrupinen (Polychaeta sedentaria). *Monatsberichte Dtsch. Akad. Wiss. Zu Berl.* 11, 517–525.
- Myrvold, K.S., Milan, J., Rasmussen, J.A., 2018. Two new finds of turtle remains from the Danian and Selandian (Paleocene) deposits of Denmark with evidence of predation by crocodilians and sharks. *Bull. Geol. Soc. Den.* 66, 211–218.
- Nagelkerken, I., Munday, P.L., 2016. Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community-level responses. *Glob. Change Biol.* 22, 974–989. <https://doi.org/10.1111/gcb.13167>.
- Nagel-Myers, J., Dietl, G.P., Brett, C.E., 2009. First report of sublethal breakage-induced predation on Devonian bivalves. *PALAIOS* 24, 460–465. <https://doi.org/10.2110/palo.2008.p08-136r>.
- Nagel-Myers, J., Dietl, G.P., Handley, J.C., Brett, C.E., 2013. Abundance is not enough: the need for multiple lines of evidence in testing for ecological stability in the fossil record. *PLoS One* 8, e63071. <https://doi.org/10.1371/journal.pone.0063071>.
- Nagle, J.S., 1964. Differential sorting of shells in the swash zone. *Biol. Bull.* 127, 353.
- Nagle, J.S., 1967. Wave and current orientation of shells. *J. Sediment. Res.* 37, 1124–1138. <https://doi.org/10.1306/74D71848-2B21-11D7-8648000102C1865D>.
- Nebelsick, J., 1995. Uses and limitations of actupaleontological investigations on echinoids. *Gebios* 28, 329–336. [https://doi.org/10.1016/S0016-6995\(95\)80178-2](https://doi.org/10.1016/S0016-6995(95)80178-2).
- Nebelsick, J.H., Kowalewski, M., 1999. Drilling predation on recent clypeasteroid echinoids from the Red Sea. *PALAIOS* 14, 127–144. <https://doi.org/10.2307/3515369>.
- Nedin, C., 1999. *Anomalocaris* predation on nonmineralized and mineralized trilobites. *Geology* 27, 987–990. [https://doi.org/10.1130/0091-7613\(1999\)027<0987:APONAM>2.3.CO;2](https://doi.org/10.1130/0091-7613(1999)027<0987:APONAM>2.3.CO;2).
- Nesbitt, E.A., 1995. Paleoeological analysis of molluscan assemblages from the middle Eocene Cowlitz Formation, southwestern Washington. *J. Paleontol.* 69, 1060–1073. <https://doi.org/10.1017/S002236600003804X>.
- Neto de Carvalho, C., Pereira, B., Klompmaker, A., Baucon, A., Moita, J.A., Pereira, P., Machado, S., Belo, J., Carvalho, J., Mergulhão, L., 2016. Running crabs, walking crinoids, grazing gastropods: behavioral diversity and evolutionary implications in the Cabeço da Ladeira Lagerstätte (Middle Jurassic, Portugal). *Comun. Geológicas* 103, 39–54.

- Neumann, C., 2000. Evidence of predation on Cretaceous sea stars from north-west Germany. *Lethaia* 33, 65–70. <https://doi.org/10.1080/00241160050150177>.
- Neumann, C., Hampe, O., 2018. Eggs for breakfast? Analysis of a probable mosasaur biting trace on the Cretaceous echinoid *Echinocorys ovata* Leske, 1778. *Foss. Rec.* 21, 55–66. <https://doi.org/10.5194/fr-21-55-2018>.
- Neumann, C., Wisshak, M., 2009. Gastropod parasitism on Late Cretaceous to Early Paleocene holasteroid echinoids - evidence from *Oichnus halo* isp. n. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 284, 115–119. <https://doi.org/10.1016/j.palaeo.2009.09.010>.
- Nicoll, R.S., 1977. Conodont apparatuses in an Upper Devonian palaeoniscoid fish from the Canning Basin, Western Australia. *BMR J. Aust. Geol. Geophys.* 2, 217–228.
- Nielsen, C., 1975. Observations on *Buccinum undatum* L. attacking bivalves and on prey responses, with a short review on attack methods of other prosobranchs. *Ophelia* 13, 87–108. <https://doi.org/10.1080/00785326.1974.10430593>.
- Nielsen, K.S.S., Nielsen, J.K., 2001. Bioerosion in Pliocene to late Holocene tests of benthic and planktonic foraminiferans, with a revision of the ichnogenus *Oichnus* and *Tremichnus*. *Ichnos* 8, 99–116. <https://doi.org/10.1080/10420940109380178>.
- Nielsen, K.S.S., Collen, J.D., Ferland, M.A., 2002. *Floresina*: a genus of predators, parasites or scavengers? *J. Foraminif. Res.* 32, 93–95. <https://doi.org/10.2113/0320093>.
- Nixon, M., 1979. Hole-boring in shells by *Octopus vulgaris* Cuvier in the Mediterranean. *Malacologia* 18, 431–443.
- Nixon, M., Maconnachie, E., 1988. Drilling by *Octopus vulgaris* (Mollusca: Cephalopoda) in the Mediterranean. *J. Zool.* 216, 687–716. <https://doi.org/10.1111/j.1469-7998.1988.tb02466.x>.
- Noriega, J.I., Cione, A.L., Aceñolaza, F.G., 2007. Shark tooth marks on Miocene balaeonotrid cetacean bones from Argentina. *Neues Jahrb. für Geol. Paläontol. Abh.* 245, 185–192. <https://doi.org/10.1127/0077-7749/2007/0245-0185>.
- Northwood, C., 2005. Early Triassic coprolites from Australia and their palaeobiological significance. *Palaeontology* 48, 49–68. <https://doi.org/10.1111/j.1475-4983.2004.00432.x>.
- Norton, S.F., 1988. Role of the gastropod shell and operculum in inhibiting predation by fishes. *Science* 241, 92–94. <https://doi.org/10.1126/science.241.4861.92>.
- Noto, C.R., Main, D.J., Drumheller, S.K., 2012. Feeding traces and paleobiology of a Cretaceous (Cenomanian) crocodyliform: example from the Woodbine Formation of Texas. *PALAIOS* 27, 105–115. <https://doi.org/10.2110/palo.2011.p11-052r>.
- Nyborg, T., Ifrim, C., Moreno-Bedmar, J.A., Múzquiz, H.P., Giersch, S., Vega, F.J., 2014. Late Cretaceous fish cans: fish preserved in ammonite body chambers from the middle Santonian of Coahuila State, northeastern Mexico. *Neues Jahrb. für Geol. Paläontol. Abh.* 273, 75–88. <https://doi.org/10.1127/0077-7749/2014/0417>.
- O'Brien, J., Van Wyk, P., 1985. Effects of crustacean parasitic castrators (epicaridean isopods and rhizocephalan barnacles) on growth of crustacean hosts. In: Wenner, A.M. (Ed.), *Factors in Adult Growth, Crustacean Issues*. vol. 3. A.A. Balkema, Rotterdam, pp. 191–218.
- Oji, T., 1996. Is predation intensity reduced with increasing depth? Evidence from the West Atlantic stalked crinoid *Endoxocrinus parvae* (Gervais) and implications for the Mesozoic marine revolution. *Paleobiology* 22, 339–351. <https://doi.org/10.1017/S0094837300016328>.
- Oji, T., Okamoto, T., 1994. Arm autotomy and arm branching pattern as anti-predatory adaptations in stalked and stalkless crinoids. *Paleobiology* 20, 27–39. <https://doi.org/10.1017/S0094837300011118>.
- Oji, T., Ogaya, C., Sato, T., 2003. Increase of shell-crushing predation recorded in fossil shell fragmentation. *Paleobiology* 29, 520–526. [https://doi.org/10.1666/0094-8373\(2003\)029<0520:IOSPRI>2.0.CO;2](https://doi.org/10.1666/0094-8373(2003)029<0520:IOSPRI>2.0.CO;2).
- Okamura, B., 1986. Group living and the effects of spatial position in aggregations of *Mytilus edulis*. *Oecologia* 69, 341–347. <https://doi.org/10.1007/BF00377054>.
- O'Keefe, F.R., Street, H.P., Cavigelli, J.P., Socha, J.J., O'Keefe, D., 2009. A plesiosaur containing an ichthyosaur embryo as stomach contents from the Sundance Formation of the Bighorn Basin, Wyoming. *J. Vertebr. Paleontol.* 29, 1306–1310. <https://doi.org/10.1671/039.029.0403>.
- Olivera, A.M., Wood, W.L., 1997. Hydrodynamics of bivalve shell entrainment and transport. *J. Sediment. Res.* 67, 514–526. <https://doi.org/10.1306/D42685B8-2B26-11D7-8648000102C1865D>.
- Orr, V., 1962. The drilling habit of *Capulus danieli* (Crosse) (Mollusca: Gastropoda). *The Veliger* 5, 63–67.
- Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R.M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R.G., Plattner, G.-K., Rodgers, K.B., Sabine, C.L., Sarmiento, J.L., Schlitzer, R., Slater, R.D., Totterdell, I.J., Weirig, M.-F., Yamanaka, Y., Yool, A., 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437, 681–686. <https://doi.org/10.1038/nature04095>.
- Ortega-Hernandez, J., Esteve, J., Butterfield, N.J., 2013. Humble origins for a successful strategy: complete enrolment in Early Cambrian olenellid trilobites. *Biol. Lett.* 9, 20130679. <https://doi.org/10.1098/rsbl.2013.0679>.
- Ortmann, C., Grieshaber, M.K., 2003. Energy metabolism and valve closure behaviour in the Asian clam *Corbicula fluminea*. *J. Exp. Biol.* 206, 4167–4178. <https://doi.org/10.1242/jeb.00656>.
- Ottens, K.J., Dietl, G.P., Kelley, P.H., Stanford, S.D., 2012. A comparison of analyses of drilling predation on fossil bivalves: bulk- vs. taxon-specific sampling and the role of collector experience. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 319–320, 84–92. <https://doi.org/10.1016/j.palaeo.2012.01.006>.
- Ozanne, C.R., Harries, P.J., 2002. Role of predation and parasitism in the extinction of the inoceramid bivalves: an evaluation. *Lethaia* 35, 1–19. <https://doi.org/10.1111/j.1502-3931.2002.tb00062.x>.
- Pahari, A., Mondal, S., Bardhan, S., Sarkar, D., Saha, S., Buragohain, D., 2016. Subaerial naticid gastropod drilling predation by *Natica tigrina* on the intertidal molluscan community of Chandipur, Eastern Coast of India. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 451, 110–123. <https://doi.org/10.1016/j.palaeo.2016.03.020>.
- Paine, R.T., 1966. Food web complexity and species diversity. *Am. Nat.* 100, 65–75. <https://doi.org/10.1086/282400>.
- Paine, R.T., 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* 57, 858–873. <https://doi.org/10.2307/1941053>.
- Palmer, A.R., 1979. Fish predation and the evolution of gastropod shell sculpture: Experimental and geographic evidence. *Evolution* 33, 697–713. <https://doi.org/10.1111/j.1558-5646.1979.tb04722.x>.
- Palmer, A.R., 1980. A Comparative and Experimental Study of Feeding and Growth in Thaidid Gastropods (Dissertation). University of Washington, Seattle.
- Palmer, A.R., 1988. Feeding biology of *Ocenebra lurida* (Prosobranchia: Muricacea): diet, predator-prey size relations, and attack behavior. *The Veliger* 31, 192–203.
- Palmer, A.R., 1992. Calcification in marine molluscs: how costly is it? *Proc. Natl. Acad. Sci.* 89, 1379–1382. <https://doi.org/10.1073/pnas.89.4.1379>.
- Parent, H., Greco, A.F., Bejas, M., 2010. Size-shape relationships in the Mesozoic planispiral ammonites. *Acta Palaeontol. Pol.* 55, 85–98. <https://doi.org/10.4202/app.2009.0066>.
- Parent, H., Westermann, G.E.G., Chamberlain, J.A., 2014. Ammonite aptychi: functions and role in propulsion. *Geobios* 47, 45–55. <https://doi.org/10.1016/j.geobios.2013.12.001>.
- Pasini, G., Garassino, A., 2012. Naticid gastropod and octopodid cephalopod predatory traces: evidence of drill holes on the leucosid crab *Ristoria pliocaenica* (Ristori, 1891), from the Pliocene of the “La Serra” quarry (Tuscany, Italy). *Atti Della Soc. Ital. Sci. Nat. e Mus. Civ. Storia Nat. Milano* 153, 257–266.
- Pastorok, R.A., 1980. The effects of predator hunger and food abundance on prey selection by *Chaoborus larvae*. *Limnol. Oceanogr.* 25, 910–921. <https://doi.org/10.4319/lo.1980.25.5.0910>.
- Pates, S., Bicknell, R.D.C., 2019. Elongated thoracic spines as potential predatory deterrents in olenelline trilobites from the Lower Cambrian of Nevada. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 516, 295–306. <https://doi.org/10.1016/j.palaeo.2018.12.013>.
- Pates, S., Bicknell, R.D.C., Daley, A.C., Zamora, S., 2017. Quantitative analysis of repaired and unrepaired damage to trilobites from the Cambrian (Stage 4, Drumian) Iberian Chains, NE Spain. *PALAIOS* 32, 750–761. <https://doi.org/10.2110/palo.2017.055>.
- Paul, S., Herbert, G.S., 2014. Plio-Pleistocene drilling predation in Florida bivalves: Predator identity, competition, and biotic change. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 404, 67–77. <https://doi.org/10.1016/j.palaeo.2014.03.040>.
- Payne, J.L., Boyer, A.G., Brown, J.H., Finnegan, S., Kowalewski, M., Krause, R.A., Lyons, S.K., McClain, C.R., McShea, D.W., Novack-Gottshall, P.M., Smith, F.A., Stempin, J.A., Wang, S.C., 2009. Two-phase increase in the maximum size of life over 3.5 billion years reflects biological innovation and environmental opportunity. *Proc. Natl. Acad. Sci.* 106, 24–27. <https://doi.org/10.1073/pnas.0806314106>.
- Payne, J.L., Heim, N.A., Knope, M.L., McClain, C.R., 2014. Metabolic dominance of bivalves predates brachiopod diversity decline by more than 150 million years. *Proc. R. Soc. B* 281, 20133122. <https://doi.org/10.1098/rspb.2013.3122>.
- Peck, L.S., 1993. The tissues of articulate brachiopods and their value to predators. *Philos. Trans. R. Soc. B Biol. Sci.* 339, 17–32. <https://doi.org/10.1098/rstb.1993.0002>.
- Peharda, M., Morton, B., 2006. Experimental prey species preferences of *Hexaplex trunculus* (Gastropoda: Muricidae) and predator-prey interactions with the Black mussel *Mytilus galloprovincialis* (Bivalvia: Mytilidae). *Mar. Biol.* 148, 1011–1019. <https://doi.org/10.1007/s00227-005-0148-5>.
- Pek, I., Mikuláš, R., 1996. The ichnogenus *Oichnus* Bromley, 1981 - predation traces in gastropod shells from the Badenian in the vicinity of Ceska Trebova (Czech Republic). *Vestník Českého Geol. Úst.* 71, 107–120.
- Perry, D.M., 1987. Optimal diet theory: Behavior of a starved predatory snail. *Oecologia* 72, 360–365. <https://doi.org/10.1007/BF00377564>.
- Person, P., Smarsh, A., Lipson, S.J., Carriker, M.R., 1967. Enzymes of the accessory boring organ of the muricid gastropod *Urosalpinx cinerea follyensis*. I. Aerobic and related oxidative systems. *Biol. Bull.* 133, 401–410. <https://doi.org/10.2307/1539835>.
- Petchey, O.L., McPhearson, P.T., Casey, T.M., Morin, P.J., 1999. Environmental warming alters food-web structure and ecosystem function. *Nature* 402, 69–72. <https://doi.org/10.1038/47023>.
- Peterson, C.H., 1982. Clam predation by whelks (*Busyon* spp.): Experimental tests of the importance of prey size, prey density, and seagrass cover. *Mar. Biol.* 66, 159–170. <https://doi.org/10.1007/BF00397189>.
- Peterson, C.H., 1991. Intertidal zonation of marine invertebrates in sand and mud. *Am. Sci.* 79, 236–249.
- Peterson, C.H., Black, R., 1995. Drilling by buccinid gastropods of the genus *Cominella* in Australia. *The Veliger* 38, 37–42.
- Pether, J., 1995. *Belichnus* new ichnogenus, a ballistic trace on mollusc shells from the Holocene of the Benguela region, South Africa. *J. Paleontol.* 69, 171–181. <https://doi.org/10.1017/S0022336000027013>.
- Petratits, P.S., 1987. Immobilization of the predatory gastropod, *Nucella lapillus*, by its prey, *Mytilus edulis*. *Biol. Bull.* 172, 307–314.
- Pianka, E.R., 1974. *Evolutionary Ecology*. Harper & Row, New York.
- Pierrehumbert, N.D., Allmon, W.D., 2018. Morphology of crab predation scars on Recent and fossil turritellid gastropods. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 497, 1–10. <https://doi.org/10.1016/j.palaeo.2018.01.032>.
- Pinna, G., Arduini, P., Pesarini, C., Teruzzi, G., 1985. Some controversial aspects of the morphology and anatomy of *Ostenocaris cypriformis* (Crustacea, Thylacocephala). *Trans. R. Soc. Edinb. Earth Sci.* 76, 373–379. <https://doi.org/10.1017/S0263593300010580>.
- Pohowsky, R.A., 1978. The boring ctenostomate Bryozoa: Taxonomy and paleobiology based on cavities in calcareous substrata. *Bull. Am. Paleontol.* 73, 1–192.

- Pollard, J.E., 1968. The gastric contents of an ichthyosaur from the Lower Lias of Lyme Regis, Dorset. *Palaeontol.* 11, 376–388.
- Ponder, W.F., Taylor, J.D., 1992. Predatory shell drilling by two species of *Austroginella* (Gastropoda: Marginellidae). *J. Zool.* 228, 317–328.
- Porter, S.M., 2016. Tiny vampires in ancient seas: evidence for predation via perforation in fossils from the 780–740 million-year-old Chuar Group, Grand Canyon, USA. *Proc. R. Soc. B Biol. Sci.* 283, 20160221. <https://doi.org/10.1098/rspb.2016.0221>.
- Portis, A., 1883. Nuovi studi sulle tracce attribuite all'uomo pliocenico. *Mem. Della Regia Accad. Delle Sci. Torino* 35, 3–27.
- Pratt, D.M., 1974. Behavioral defenses of *Crepidula fornicata* against attack by *Urosalpinx cinerea*. *Mar. Biol.* 27, 47–49. <https://doi.org/10.1007/BF00394759>.
- Pratt, B.R., 1998. Probable predation on Upper Cambrian trilobites and its relevance for the extinction of soft-bodied Burgess Shale-type animals. *Lethaia* 31, 73–88. <https://doi.org/10.1111/j.1502-3931.1998.tb00493.x>.
- Preston, S.J., Roberts, D., Montgomery, W.I., 1993. Shell scarring in *Calliostoma zizyphinum* (Prosobranchia: Trochidae) from Strangford Lough, Northern Ireland. *J. Molluscan Stud.* 59, 211–222. <https://doi.org/10.1093/mollus/59.2.211>.
- Pruden, M.J., Mendonca, S.E., Leighton, L.R., 2018. The effects of predation on the preservation of ontogenetically young individuals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 490, 404–414. <https://doi.org/10.1016/j.palaeo.2017.11.019>.
- Pulliam, H.R., 1974. On the theory of optimal diets. *Am. Nat.* 108, 59–74. <https://doi.org/10.1086/282885>.
- Quaresma, V. da S., Amos, C.L., Bastos, A.C., 2007. The influence of articulated and disarticulated cockle shells on the erosion of a cohesive bed. *J. Coast. Res.* 236, 1443–1451. <https://doi.org/10.2112/05-0449.1>.
- Raffaelli, D.G., 1978. The relationship between shell injuries, shell thickness and habitat characteristics of the intertidal snail *Littorina rudis* Maton. *J. Molluscan Stud.* 44, 166–170.
- Ramsay, K., Richardson, C.A., Kaiser, M.J., 2001. Causes of shell scarring in dog cockles *Glycymeris glycymeris* L. *J. Sea Res.* 45, 131–139. [https://doi.org/10.1016/S1385-1101\(01\)00050-8](https://doi.org/10.1016/S1385-1101(01)00050-8).
- Rasser, M.W., Covich, A.P., 2014. Predation on freshwater snails in Miocene Lake Steinheim: a trigger for intralacustrine evolution? *Lethaia* 47, 524–532. <https://doi.org/10.1111/let.12078>.
- Reboullet, S., Rard, A., 2008. Double alignments of ammonoid aptychi from the Lower Cretaceous of southeast France: result of a post-mortem transport or bromalites? *Acta Palaeontol. Pol.* 53, 261–274. <https://doi.org/10.4202/app.2008.0207>.
- Reich, S., Di Martino, E., Todd, J.A., Wesselingh, F.P., Renema, W., 2015. Indirect paleo-seagrass indicators (IPSI): a review. *Earth-Sci. Rev.* 143, 161–186. <https://doi.org/10.1016/j.earscirev.2015.01.009>.
- Reid, M., Taylor, W.L., Brett, C.E., Hunter, A.W., Bordy, E.M., 2019. Taphonomy and paleoecology of an ophiuroid-stylophoran obrution deposit from the lower devonian bokkeveld group, South Africa. *PALAIOS* 34, 212–228. <https://doi.org/10.2110/palo.2018.048>.
- Reolid, M., Molina, J.M., 2010. Serpulid-*Frutitextes* assemblage from shadow-cryptic environments in Jurassic marine caves, Betic Cordillera, southern Spain. *PALAIOS* 25, 468–474. <https://doi.org/10.2110/palo.2009.p09-150r>.
- Reyment, R.A., Elewa, A.M.T., 2003. Predation by drills on Ostracoda. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 93–111. https://doi.org/10.1007/978-1-4615-0161-9_5.
- Reyment, R.A., Reyment, E.R., Honigstein, A., 1987. Predation by boring gastropods on Late Cretaceous and Early Palaeocene ostracods. *Cretac. Res.* 8, 189–209. [https://doi.org/10.1016/0195-6671\(87\)90021-8](https://doi.org/10.1016/0195-6671(87)90021-8).
- Rhoads, D.C., Lutz, R.A., Cerrato, R.M., Revelas, E.C., 1982. Growth and predation activity at deep-sea hydrothermal vents along the Galapagos Rift. *J. Mar. Res.* 40, 503–516.
- Richards, L.J., 1983. Hunger and the optimal diet. *Am. Nat.* 122, 326–334. <https://doi.org/10.1086/284138>.
- Richards, E.J., Leighton, L.R., 2012. Size refugia from predation through time: a case-study of two Middle Devonian brachiopod genera. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 363–364, 163–171. <https://doi.org/10.1016/j.palaeo.2012.09.012>.
- Richards, R.P., Shabica, C.W., 1969. Cylindrical living burrows in Ordovician dalmanellid brachiopod beds. *J. Paleontol.* 43, 838–841.
- Ricker, W.E., 1941. The consumption of young sockeye salmon by predaceous fish. *J. Fish. Res. Board Can.* 5B, 293–313. <https://doi.org/10.1139/f40-033>.
- Riedel, B., Stachowitsch, M., Zuschin, M., 2008a. Sea anemones and brittle stars: unexpected predatory interactions during induced in situ oxygen crises. *Mar. Biol.* 153, 1075–1085. <https://doi.org/10.1007/s00227-007-0880-0>.
- Riedel, B., Zuschin, M., Haselmair, A., Stachowitsch, M., 2008b. Oxygen depletion under glass: behavioural responses of benthic macrofauna to induced anoxia in the Northern Adriatic. *J. Exp. Mar. Biol. Ecol.* 367, 17–27. <https://doi.org/10.1016/j.jembe.2008.08.007>.
- Riedel, B., Zuschin, M., Stachowitsch, M., 2012. Tolerance of benthic macrofauna to hypoxia and anoxia in shallow coastal seas: a realistic scenario. *Mar. Ecol. Prog. Ser.* 458, 39–52. <https://doi.org/10.3354/meps09724>.
- Ries, J.B., Cohen, A.L., McCorkle, D.C., 2009. Marine calcifiers exhibit mixed responses to CO₂-induced ocean acidification. *Geology* 37, 1131–1134. <https://doi.org/10.1130/G30210A.1>.
- Robba, E., Ostinelli, F., 1975. Studi paleoecologici sul Pliocene Ligure: pt. 1, Testimonianze di predazione sui molluschi Pliocenici di Albenga. *Riv. Ital. Paleontol. E Stratigr.* 81, 309–372.
- Robinson, J.H., 2014. Repair of gastropod drillholes in a platydid brachiopod from Fiordland, New Zealand. *Lethaia* 47, 31–37. <https://doi.org/10.1111/let.12035>.
- Robles, C., 1987. Predator foraging characteristics and prey population structure on a sheltered shore. *Ecology* 68, 1502–1514. <https://doi.org/10.2307/1939234>.
- Rodrigues, C.L., Nojima, S., Kikuchi, T., 1987. Mechanics of prey size preference in the gastropod *Neverita didyma* preying on the bivalve *Ruditapes philippinarum*. *Mar. Ecol. Prog. Ser.* 40, 87–93.
- Rohr, D.M., 1976. Silurian predator borings in the brachiopod *Dicaelosis* from the Canadian Arctic. *J. Paleontol.* 50, 1175–1179.
- Rojas, A., Verde, M., Urteaga, D., Scarabino, F., Martinez, S., 2014. The first predatory drillhole on a fossil chiton plate: an occasional prey item or an erroneous attack? *PALAIOS* 29, 414–419. <https://doi.org/10.2110/palo.2014.030>.
- Rojas, A., Portell, R.W., Kowalewski, M., 2017. The post-Palaeozoic fossil record of drilling predation on lingulide brachiopods. *Lethaia* 50, 296–305. <https://doi.org/10.1111/let.12198>.
- Roopnarine, P.D., Beussink, A., 1999. Extinction and naticid predation of the bivalve *Chione* von Mühlfeld in the late Neogene of Florida. *Palaeontol. Electron.* 2, 24. <https://palaeo-electronica.org/content/2/1-bivalve>.
- Rothschild, B.M., Clark, N.D.L., Clark, C.M., 2018. Evidence for survival in a Middle Jurassic plesiosaur with a humeral pathology: what can we infer of plesiosaur behaviour? *Palaeontol. Electron.* 21.1.13A 1–11. <https://doi.org/10.26879/719>.
- Rovero, F., Hughes, R.N., Chelazzi, G., 1999. Cardiac and behavioural responses of mussels to risk of predation by dogwhelks. *Anim. Behav.* 58, 707–714. <https://doi.org/10.1006/anbe.1999.1176>.
- Roy, K., 1996. The roles of mass extinction and biotic interaction in large-scale replacements: a reexamination using the fossil record of stromboidean gastropods. *Paleobiology* 22, 436–452. <https://doi.org/10.1017/S0094837300016389>.
- Roy, K., Miller, D.J., LaBarbera, M., 1994. Taphonomic bias in analyses of drilling predation: Effects of gastropod drill holes on bivalve shell strength. *PALAIOS* 9, 413–421. <https://doi.org/10.2307/3515059>.
- Ruiz, F.R., Abad, M., García, E.X., Toscano, A., Prudencio, M.I., Dias, M.I., Galán, E., 2010a. Evidencias de depredación en ostrácodos holocenos del Parque Nacional de Doñana (SO de España). *Rev. Esp. Micropaleontol.* 42, 267–273.
- Ruiz, F.R., Abad, M., González-Regalado, M.L., Civis, J., González-Regalado, J.A., García, E.X., Toscano, A., 2010b. Predation on Neogene ostracods of Southwestern Spain. *Riv. Ital. Paleontol. E Stratigr.* 16, 253–260.
- Runham, N.W., Bailey, C.J., Carr, M., Evans, C.A., Malham, S., 1997. Hole drilling in crab and gastropod shells by *Eledone cirrhosa* (Lamarck, 1798). *Sci. Mar.* 61, 67–76.
- von Rütten-Kositzkau, B., 1999. Taphonomie und Biogeographie des hartteiltragenden Makrobenthos im Tiefwasser des Roten Meeres. *Beringeria* 24, 2–150.
- Sahling, H., Galkin, S.V., Salyuk, A., Greinert, J., Foerster, H., Piepenburg, D., Suess, E., 2003. Depth-related structure and ecological significance of cold-seep communities - a case study from the Sea of Okhotsk. *Deep-Sea Res. I* 50, 1391–1409. <https://doi.org/10.1016/j.dsr.2003.08.004>.
- Salamon, M., Gorzelak, P., 2010. Late Cretaceous crinoids (Crinoidea) from Eastern Poland. *Palaeontogr. Abt. A* 291, 1–43. <https://doi.org/10.1127/pala/291/2010/1>.
- Salamon, M.A., Niedzwiedzki, R., Gorzelak, P., Lach, R., Surnik, D., 2012. Bromalites from the Middle Triassic of Poland and the rise of the Mesozoic Marine Revolution. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 321–322, 142–150. <https://doi.org/10.1016/j.palaeo.2012.01.029>.
- Salamon, M.A., Gorzelak, P., Niedzwiedzki, R., Trzęsiok, D., Baumiller, T.K., 2014. Trends in shell fragmentation as evidence of mid-Paleozoic changes in marine predation. *Paleobiology* 40, 14–23. <https://doi.org/10.1666/13018>.
- Saloom, M.E., Scot Duncan, R., 2005. Low dissolved oxygen levels reduce anti-predation behaviours of the freshwater clam *Corbicula fluminea*. *Freshw. Biol.* 50, 1233–1238. <https://doi.org/10.1111/j.1365-2427.2005.01396.x>.
- Sanchez-Salazar, M.E., Griffiths, C.L., Seed, R., 1987. The effect of size and temperature on the predation of cockles *Cerastoderma edule* (L.) by the shore crab *Carcinus maenas* (L.). *J. Exp. Mar. Biol. Ecol.* 111, 181–193. [https://doi.org/10.1016/0022-0981\(87\)90054-2](https://doi.org/10.1016/0022-0981(87)90054-2).
- Sander, F., Lalli, C.M., 1982. A comparative study of mollusk communities on the shelf-slope margin of Barbados, West Indies. *The Veliger* 24, 309–318.
- Sanford, E., 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283, 2095–2097. <https://doi.org/10.1126/science.283.5410.2095>.
- Sanford, E., 2002. Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. *Integr. Comp. Biol.* 42, 881–891. <https://doi.org/10.1093/icb/42.4.881>.
- Sanford, E., Gaylord, B., Hettlinger, A., Lenz, E.A., Meyer, K., Hill, T.M., 2014. Ocean acidification increases the vulnerability of native oysters to predation by invasive snails. *Proc. R. Soc. B Biol. Sci.* 281, 20132681. <https://doi.org/10.1098/rspb.2013.2681>.
- Sato, T., Tanabe, K., 1998. Cretaceous plesiosaurs ate ammonites. *Nature* 394, 629–630. <https://doi.org/10.1038/29199>.
- Saunders, W.B., Wehman, D.A., 1977. Shell strength of *Nautilus* as a depth limiting factor. *Paleobiology* 3, 83–89. <https://doi.org/10.1017/S0094837300005133>.
- Saunders, W.B., Knight, R.L., Bond, P.N., 1991. *Octopus* predation on *Nautilus*: evidence from Papua New Guinea. *Bull. Mar. Sci.* 49, 280–287.
- Savarese, M., 1994. Taphonomic and paleoecologic implications of flow-induced forces on concavo-convex articulate brachiopods: an experimental approach. *Lethaia* 27, 301–312. <https://doi.org/10.1111/j.1502-3931.1994.tb01579.x>.
- Savazzi, E., 1984a. Adaptive significance of shell torsion in mytilid bivalves. *Palaeontology* 27, 307–314.
- Savazzi, E., 1984b. Functional morphology and autecology of *Pseudoptera* (bakevelliid bivalves, Upper Cretaceous of Portugal). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 46, 313–324. [https://doi.org/10.1016/0031-0182\(84\)90004-X](https://doi.org/10.1016/0031-0182(84)90004-X).
- Savazzi, E., 1999. Boring, nestling and tube-building bivalves. In: Savazzi, E. (Ed.), *Functional Morphology of the Invertebrate Skeleton*. Wiley, Chichester, pp. 205–237.
- Savazzi, E., Reyment, R.A., 1989. Subaerial hunting behaviour in *Natica guateriana* (naticid gastropod). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 74, 355–364. [https://doi.org/10.1016/0167-0607\(89\)90004-X](https://doi.org/10.1016/0167-0607(89)90004-X).

- doi.org/10.1016/0031-0182(89)90070-9.
- Sawyer, J.A., Zuschin, M., 2010. Intensities of drilling predation of molluscan assemblages along a transect through the northern Gulf of Trieste (Adriatic Sea). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 285, 152–173. <https://doi.org/10.1016/j.palaeo.2009.11.007>.
- Sawyer, J.A., Zuschin, M., 2011. Drilling predation in mollusks from the Lower and Middle Miocene of the Central Paratethys. *PALAIOS* 26, 284–297. <https://doi.org/10.2110/palo.2009.p09-161r>.
- Sawyer, J.A., Zuschin, M., Riedel, B., Stachowitsch, M., 2009. Predator–prey interactions from in situ time-lapse observations of a sublittoral mussel bed in the Gulf of Trieste (Northern Adriatic). *J. Exp. Mar. Biol. Ecol.* 371, 10–19. <https://doi.org/10.1016/j.jembe.2008.12.010>.
- Schiaparelli, S., Ghirardo, C., Bohn, J., Chiantore, M., Albertelli, G., Cattaneo-Vietti, R., 2007. Antarctic associations: the parasitic relationship between the gastropod *Bathyrinicola tumidula* (Thiele, 1912) (Ptenoglossa: Eulimidae) and the comatulid *Notocrinus virilis* Mortensen, 1917 (Crinoidea: Notocrinidae) in the Ross Sea. *Polar Biol.* 30, 1545–1555. <https://doi.org/10.1007/s00300-007-0315-x>.
- Schiffbauer, J.D., Yanes, Y., Tyler, C.L., Kowalewski, M., Leighton, L.R., 2008. The microstructural record of predation: a new approach for identifying predatory drill holes. *PALAIOS* 23, 810–820. <https://doi.org/10.2110/palo.2008.p08-045r>.
- Schiffbauer, J.D., Huntley, J.W., O'Neil, G.R., Darroch, S.A.F., Laflamme, M., Cai, Y., 2016. The latest Ediacaran wormworld fauna: setting the ecological stage for the Cambrian Explosion. *GSA Today* 26, 4–11. <https://doi.org/10.1130/GSATG265A.1>.
- Schimmel, M.K., Kowalewski, M., Coffey, B.P., 2012. Traces of predation/parasitism recorded in Eocene brachiopods from the Castle Hayne Limestone, North Carolina, USA. *Lethaia* 45, 274–289. <https://doi.org/10.1111/j.1502-3931.2011.00281.x>.
- Schindler, D.E., Johnson, B.M., MacKay, N.A., Bouwes, N., Kitchell, J.F., 1994. Crab: snail size-structured interactions and salt marsh predation gradients. *Oecologia* 97, 49–61. <https://doi.org/10.1007/BF00317908>.
- Schmidt, N., 1989. Paleobiological implications of shell repair in Recent marine gastropods from the northern Gulf of California. *Hist. Biol.* 3, 127–139. <https://doi.org/10.1080/08912968909386517>.
- Schmitz, O., 2005. Behavior of predators and prey and links with population-level processes. In: Barbosa, P., Castellanos, I. (Eds.), *Ecology of Predator-Prey Interactions*. Oxford University Press, New York, pp. 256–278.
- Schoener, T.W., 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2, 369–404.
- Schulz, M., 2002. *Krebse aus dem Oberen Muschelkalk von Ostthessen und Thüringen. Teil I: Pseudopemphix albertii* (H. v. Meyer, 1840). Veröff. Naturkundemuseum Erfurt 21, 15–38.
- Schweitzer, C.E., Feldmann, R.M., 2010. The Decapoda (Crustacea) as predators on Mollusca through geologic time. *PALAIOS* 25, 167–182. <https://doi.org/10.2110/palo.2009.p09-054r>.
- Schwimmer, D.R., Stewart, J.D., Williams, G.D., 1997. Scavenging by sharks of the genus *Squalicorax* in the Late Cretaceous of North America. *PALAIOS* 12, 71–83. <https://doi.org/10.2307/3515295>.
- Seilacher, A., 1993. Ammonite aptychi; how to transform a jaw into an operculum? *Am. J. Sci.* 293, 20–32. <https://doi.org/10.2475/ajs.293.A.20>.
- Selly, T., Huntley, J.W., Shelton, K.L., Schiffbauer, J.D., 2016. Ichnofossil record of selective predation by Cambrian trilobites. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 444, 38–38. <https://doi.org/10.1016/j.palaeo.2015.11.033>.
- Selly, T., Hale, K.E., Schiffbauer, J.D., Clapp, D.A., Huntley, J.W., 2018. The influence of environmental gradients on molluscan diversity, community structure, body size, and predation in a carbonate tidal creek, San Salvador (The Bahamas). *Am. J. Sci.* 318, 246–273. <https://doi.org/10.2475/02.2018.03>.
- Shanks, A.L., Wright, W.G., 1986. Adding teeth to wave action: the destructive effects of wave-borne rocks on intertidal organisms. *Oecologia* 69, 420–428. <https://doi.org/10.1007/BF00377065>.
- Sheehan, P.M., Lesperance, P.J., 1978. Effect of predation on the population dynamics of a Devonian brachiopod. *J. Paleontol.* 52, 812–817.
- Sherker, Z.T., Ellrich, J.A., Scrosati, R.A., 2017. Predator-induced shell plasticity in mussels hinders predation by drilling snails. *Mar. Ecol. Prog. Ser.* 573, 167–175. <https://doi.org/10.3354/meps12194>.
- Shoji, J., Masuda, R., Yamashita, Y., Tanaka, M., 2005. Effect of low dissolved oxygen concentrations on behavior and predation rates on red sea bream *Pagrus major* larvae by the jellyfish *Aurelia aurita* and by juvenile Spanish mackerel *Scomberomorus niphonius*. *Mar. Biol.* 147, 863–868. <https://doi.org/10.1007/s00227-005-1579-8>.
- Sievers, D., Nebelsick, J.H., 2018. Fish predation on a Mediterranean echinoid: Identification and preservation potential. *PALAIOS* 33, 47–54. <https://doi.org/10.2110/palo.2017.041>.
- Signor, P.W., Brett, C.E., 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology* 10, 229–245. <https://doi.org/10.1017/S0094837300008174>.
- Sime, J.A., Kelley, P.H., 2016. Common mollusk genera indicate interactions with their predators were ecologically stable across the Plio-Pleistocene extinction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 463, 216–229. <https://doi.org/10.1016/j.palaeo.2016.10.012>.
- Simões, M.G., Rodrigues, S.C., Kowalewski, M., 2007. Comparative analysis of drilling frequencies in Recent brachiopod-mollusk associations from the southern Brazilian shelf. *PALAIOS* 22, 143–154. <https://doi.org/10.2110/palo.2006.p06-040r>.
- Skovsted, C.B., 2004. Mollusc fauna of the Early Cambrian Bastion Formation of north-east Greenland. *Bull. Geol. Soc. Den.* 51, 11–37.
- Skovsted, C.B., Brock, G.A., Lindström, A., Peel, J.S., Paterson, J.R., Fuller, M.K., 2007. Early Cambrian record of failed durophagy and shell repair in an epibenthic mollusc. *Biol. Lett.* 3, 314–317. <https://doi.org/10.1098/rsbl.2007.0006>.
- Sliter, W.V., 1971. Predation on benthic foraminifers. *J. Foraminif. Res.* 1, 20–29. <https://doi.org/10.2113/gsjfr.1.1.20>.
- Sliter, W.V., 1975. Foraminiferal life and residue assemblages from Cretaceous slope deposits. *Geol. Soc. Am. Bull.* 86, 897–906. [https://doi.org/10.1130/0016-7606\(1975\)86<897:FLARAF>2.0.CO;2](https://doi.org/10.1130/0016-7606(1975)86<897:FLARAF>2.0.CO;2).
- Smith, J.M., 1976. Evolution and the theory of games: in situations characterized by conflict of interest, the best strategy to adopt depends on what others are doing. *Am. Sci.* 64, 41–45.
- Smith, L.D., Jennings, J.A., 2000. Induced defensive responses by the bivalve *Mytilus edulis* to predators with different attack modes. *Mar. Biol.* 136, 461–469. <https://doi.org/10.1007/s002270050705>.
- Smith, S.A., Thayer, C.W., Brett, C.E., 1985. Predation in the Paleozoic: Gastropod-like drillholes in Devonian brachiopods. *Science* 230, 1033–1035. <https://doi.org/10.1126/science.230.4729.1033>.
- Smith, K.E., Aronson, R.B., Steffel, B.V., Amsler, M.O., Thatje, S., Singh, H., Anderson, J., Brothers, C.J., Brown, A., Ellis, D.S., Havenhand, J.N., James, W.R., Moksnes, P.-O., Randolph, A.W., Sayre-McCord, T., McClintock, J.B., 2017. Climate change and the threat of novel marine predators in Antarctica. *Ecosphere* 8, e02017. <https://doi.org/10.1002/ecs2.2017>.
- Smith, J.A., Hensley, J.C., Dietl, G.P., 2018. On drilling frequency and Manly's alpha: towards a null model for predator preference in paleoecology. *PALAIOS* 33, 61–68. <https://doi.org/10.2110/palo.2017.098>.
- Smith, J.A., Dietl, G.P., Handley, J.C., 2019. Durophagy bias: the effect of shell destruction by crushing predators on drilling frequency. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 514, 690–694. <https://doi.org/10.1016/j.palaeo.2018.11.019>.
- Snelgrove, P.V.R., 1999. Getting to the bottom of marine biodiversity: sedimentary habitats. *BioScience* 49, 129–138. <https://doi.org/10.2307/1313538>.
- Sperling, E.A., Frieder, C.A., Raman, A.V., Girguis, P.R., Levin, L.A., Knoll, A.H., 2013. Oxygen, ecology, and the Cambrian radiation of animals. *Proc. Natl. Acad. Sci.* 110, 13446–13451. <https://doi.org/10.1073/pnas.1312781110>.
- Stafford, E.S., Leighton, L.R., 2011. Vermeij Crushing Analysis: a new old technique for estimating crushing predation in gastropod assemblages. *Palaeoclimatol. Palaeoecol.* 305, 123–137. <https://doi.org/10.1016/j.palaeo.2011.02.026>.
- Stafford, E.S., Dietl, G.P., Gingras, M.P., Leighton, L.R., 2015. *Caedichnus*, a new ichnogenus representing predatory attack on the gastropod shell aperture. *Ichnos* 22, 87–102. <https://doi.org/10.1080/10420940.2015.1031899>.
- Stanley, S.M., 2008. Predation defeats competition on the seafloor. *Paleobiology* 34, 1–21. <https://doi.org/10.1666/07026.1>.
- Stanton, R.J., Nelson, P.C., 1980. Reconstruction of the trophic web in paleontology: Community structure in the Stone City Formation (Middle Eocene, Texas). *J. Paleontol.* 54, 118–135.
- Stenzler, D., Atema, J., 1977. Alarm response of the marine mud snail, *Nassarius obsoletus*: Specificity and behavioral priority. *J. Chem. Ecol.* 3, 159–171. <https://doi.org/10.1007/BF00994143>.
- Stephens, D.W., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press, Princeton.
- Stewart, J.D., 1990. Preliminary account of holecostome-inoceramid commensalism in the Upper Cretaceous of Kansas. In: Boucot, A.J. (Ed.), *Evolutionary Paleobiology of Behaviour and Coevolution*. Elsevier, Amsterdam, pp. 51–57.
- Stewart, M.J., Creese, R.G., 2004. Feeding ecology of whelks on an intertidal sand flat in north-eastern New Zealand. *N. Z. J. Mar. Freshw. Res.* 38, 819–831. <https://doi.org/10.1080/00288330.2004.9517281>.
- Stone, H.M.I., 1998. On predator deterrence by pronounced shell ornament in epifaunal bivalves. *Paleontology* 41, 1051–1068.
- Strugnell, J., Jackson, J., Drummond, A.J., Cooper, A., 2006. Divergence time estimates for major cephalopod groups: evidence from multiple genes. *Cladistics* 22, 89–96. <https://doi.org/10.1111/j.1096-0031.2006.00086.x>.
- Stump, T.E., 1975. Pleistocene molluscan paleoecology and community structure of the Puerto Libertad region, Sonora, Mexico. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 17, 177–226. [https://doi.org/10.1016/0031-0182\(75\)90023-1](https://doi.org/10.1016/0031-0182(75)90023-1).
- Sutton, M.D., 2008. Tomographic techniques for the study of exceptionally preserved fossils. *Proc. R. Soc. B Biol. Sci.* 275, 1587–1593. <https://doi.org/10.1098/rspb.2008.0263>.
- Sutton, M.D., Briggs, D.E.G., Siveter, D.J., Siveter, D.J., 2006. Fossilized soft tissues in a Silurian platyceratid gastropod. *Proc. R. Soc. B Biol. Sci.* 273, 1039–1044. <https://doi.org/10.1098/rspb.2005.3403>.
- Syed, R., Sarkar, S., Sengupta, S., 2014. Predatory drilling in Tertiary larger Foraminifera from India. *Curr. Sci.* 106, 1130–1133.
- Syverson, V.J.P., Brett, C.E., Gahn, F.J., Baumiller, T.K., 2018. Spinosity, regeneration, and targeting among Paleozoic crinoids and their predators. *Paleobiology* 44, 290–305. <https://doi.org/10.1017/pab.2017.38>.
- Tackett, L.S., Tintori, A., 2019. Low drilling frequency in Norian benthic assemblages from the southern Italian Alps and the role of specialized durophages during the Late Triassic. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 513, 25–34. <https://doi.org/10.1016/j.palaeo.2018.06.034>.
- Takeda, Y., Tanabe, K., Sasaki, T., Landman, N.H., 2016. Durophagous predation on scaphitid ammonoids in the Late Cretaceous Western Interior Seaway of North America. *Lethaia* 49, 28–42. <https://doi.org/10.1111/let.12130>.
- Tanabe, K., Kruta, I., Landman, N.H., 2015. Ammonoid buccal mass and jaw apparatus. In: Klug, C., Korn, D., De Baets, K., Kruta, I., Mapeis, R.H. (Eds.), *Ammonoid Paleobiology: From Anatomy to Ecology, Topics in Geobiology*. Springer, Dordrecht, pp. 429–484. https://doi.org/10.1007/978-94-017-9630-9_10.

- Tapanila, L., 2005. Palaeoecology and diversity of endosymbionts in Palaeozoic marine invertebrates: Trace fossil evidence. *Lethaia* 38, 89–99. <https://doi.org/10.1080/002411605100013123>.
- Tapanila, L., Ferguson, A., Roberts, E.M., 2015. Paradox of drilled devil's toenails: Taphonomic mixing obscures Cretaceous drilling predation in Utah oysters. *PALAIOS* 30, 294–303. <https://doi.org/10.2110/palo.2014.058>.
- Tarhan, L.G., Jensen, S., Droser, M.L., 2012. Furrows and firmgrounds: evidence for predation and implications for Palaeozoic substrate evolution in *Rusophycus* burrows from the Silurian of New York. *Lethaia* 45, 329–341. <https://doi.org/10.1111/j.1502-3931.2011.00286.x>.
- Taylor, J.D., 1970. Feeding habits of predatory gastropods in a Tertiary (Eocene) molluscan assemblage from the Paris Basin. *Palaeontology* 13, 254–260.
- Taylor, P.D., 1982. Probable predatory borings in Late Cretaceous bryozoans. *Lethaia* 15, 67–74. <https://doi.org/10.1111/j.1502-3931.1982.tb01976.x>.
- Taylor, P.D., Palmer, T.J., 1994. Submarine caves in a Jurassic reef (La Rochelle, France) and the evolution of cave biotas. *Naturwissenschaften* 81, 357–360.
- Taylor, P.D., Wilson, M.A., 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth-Sci. Rev.* 62, 1–103. [https://doi.org/10.1016/S0012-8252\(02\)00131-9](https://doi.org/10.1016/S0012-8252(02)00131-9).
- Taylor, J.D., Cleevely, R.J., Morris, N.J., 1983. Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England. *Palaeontology* 26, 521–553.
- Taylor, M.A., Norman, D.B., Cruickshank, A.R.I., 1993. Remains of an ornithischian dinosaur in a plesiosaur from the Kimmeridgian of England. *Palaeontology* 36, 357–360.
- Thatje, S., Anger, K., Calcagno, J.A., Lovrich, G.A., Pörtner, H.-O., Arntz, W.E., 2005. Challenging the cold: Crabs reconquer the Antarctic. *Ecology* 86, 619–625. <https://doi.org/10.1890/04-0620>.
- Thayer, C.W., 1983. Sediment-mediated biological disturbance and the evolution of marine benthos. In: Tevesz, M.J.S., McCall, P.L. (Eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*. Springer US, Boston, MA, pp. 479–625. https://doi.org/10.1007/978-1-4757-0740-3_11.
- Thayer, C.W., 1985. Brachiopods versus mussels: competition, predation, and palatability. *Science* 228, 1527–1528. <https://doi.org/10.1126/science.228.4707.1527>.
- Thayer, C.W., Allmon, R.A., 1990. Unpalatable thecideid brachiopods from Palau: Ecological and evolutionary implications. In: MacKinnon, D.I., Lee, D.E., Campbell, J.D. (Eds.), *Brachiopods Through Time*. A.A. Balkema, Rotterdam, pp. 253–260.
- Thomas, R.D.K., 1976. Gastropod predation on sympatric Neogene species of *Glycymeris* (Bivalvia) from the eastern United States. *J. Paleontol.* 50, 488–499.
- Thomka, J.R., Eddy, D.B., 2018. Repeated regeneration of crinoid spines in the Upper Pennsylvanian of eastern Ohio: evidence of elevated predation intensity and significance for predator-driven evolution of crinoid morphology. *PALAIOS* 33, 508–513. <https://doi.org/10.2110/palo.2018.058>.
- Thuy, B., Gale, A.S., Kroh, A., Kucera, M., Numberger-Thuy, L.D., Reich, M., Stöhr, S., 2012. Ancient origin of the modern deep-sea fauna. *PLoS One* 7, e46913. <https://doi.org/10.1371/journal.pone.0046913>.
- Todd, J.A., Harper, E.M., 2011. Stereotypic boring behaviour inferred from the earliest known octopod feeding traces: Early Eocene, southern England. *Lethaia* 44, 214–222. <https://doi.org/10.1111/j.1502-3931.2010.00237.x>.
- Tomašových, A., Zuschin, M., 2009. Variation in brachiopod preservation along a carbonate shelf-basin transect (Red Sea and Gulf of Aden): environmental sensitivity of taphofacies. *PALAIOS* 24, 697–716. <https://doi.org/10.2110/palo.2009.p09-018r>.
- Topper, T.P., Skovsted, C.B., 2017. Keeping a lid on it: muscle scars and the mystery of the Mobergellidae. *Zool. J. Linnean Soc.* 180, 717–731. <https://doi.org/10.1093/zoolinnean/zlw011>.
- Trewin, N.H., Welsh, W., 1972. Transport, breakage and sorting of the bivalve *Macra corallina* on Aberdeen Beach, Scotland. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 12, 193–204. [https://doi.org/10.1016/0031-0182\(72\)90059-4](https://doi.org/10.1016/0031-0182(72)90059-4).
- Trussell, G.C., Matassa, C.M., Luttbeg, B., 2011. The effects of variable predation risk on foraging and growth: less risk is not necessarily better. *Ecology* 92, 1799–1806. <https://doi.org/10.1890/10.1890/10.2222.1>.
- Tschanz, K., 1989. *Lariosaurus buzzii* n. sp. from the Middle Jurassic of Monte San Giorgio (Switzerland), with comments on the classification of nothosaurs. *Palaeontographica* A208, 153–179.
- Tsujita, C.J., Westermann, G.E.G., 2001. Were limpets or mosasaur responsible for the perforations in the ammonite *Platoniceras*? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 169, 245–270. [https://doi.org/10.1016/S0031-0182\(01\)00220-6](https://doi.org/10.1016/S0031-0182(01)00220-6).
- Turra, A., Denadai, M.R., Leite, F.P.P., 2005. Predation on gastropods by shell-breaking crabs: Effects on shell availability to hermit crabs. *Mar. Ecol. Prog. Ser.* 286, 279–291. <https://doi.org/10.3354/meps286279>.
- Tuura, M.E., Baumiller, T.K., McNamara, K.J., 2008. Drill holes in Australian Cainozoic brachiopods. *Hist. Biol.* 20, 203–212. <https://doi.org/10.1080/08912960802580154>.
- Tyler, C.L., Kowalewski, M., 2014. Utility of marine benthic associations as a multivariate proxy of paleobathymetry: a direct test from Recent coastal ecosystems of North Carolina. *PLoS One* 9, e95711. <https://doi.org/10.1371/journal.pone.0095711>.
- Tyler, C.L., Schiffbauer, J.D., 2012. The fidelity of microstructural drilling predation traces to gastropod radula morphology: Paleoeological applications. *PALAIOS* 27, 658–666. <https://doi.org/10.2110/palo.2012.p12-014r>.
- Tyler, C.L., Leighton, L.R., Carlson, S.J., Huntley, J.W., Kowalewski, M., 2013. Predation on modern and fossil brachiopods: Assessing chemical defenses and palatability. *PALAIOS* 28, 724–735. <https://doi.org/10.2110/palo.2013.p13-037r>.
- Tyler, C.L., Leighton, L.R., Kowalewski, M., 2014. The effects of limpet morphology on predation by adult cancrinid crabs. *J. Exp. Mar. Biol. Ecol.* 451, 9–15. <https://doi.org/10.1016/j.jembe.2013.10.022>.
- Tyler, C.L., Dexter, T.A., Portell, R.W., Kowalewski, M., 2018. Predation-facilitated preservation of echinoids in a tropical marine environment. *PALAIOS* 33, 478–486. <https://doi.org/10.2110/palo.2018.046>.
- Underwood, C.J., 1993. The position of graptolites within Lower Palaeozoic planktic ecosystems. *Lethaia* 26, 189–202. <https://doi.org/10.1111/j.1502-3931.1993.tb01517.x>.
- Urrutia, G.X., Navarro, J.M., 2001. Patterns of shell penetration by *Chorus giganteus* juveniles (Gastropoda: Muricidae) on the mussel *Semimytilus algosus*. *J. Exp. Mar. Biol. Ecol.* 258, 141–153. [https://doi.org/10.1016/S0022-0981\(00\)00349-X](https://doi.org/10.1016/S0022-0981(00)00349-X).
- Vale, F.K., Rex, M.A., 1988. Repaired shell damage in deep-sea prosobranch gastropods from the western North Atlantic. *Malacologia* 28, 65–79.
- Vale, F.K., Rex, M.A., 1989. Repaired shell damage in a complex of rissoid gastropods from the upper continental slope south of New England. *The Nautilus* 103, 105–108.
- Vallon, L., Rindsberg, A., Martin, A., 2015. The use of the terms trace, mark and structure. *Ann. Soc. Geol. Pol.* 85, 527–528. <https://doi.org/10.14241/asgp.2015.014>.
- Van Schooten, S., 1998. *Pelecypoda polytropia nystii*. *Afzettingen* 19, 6–8.
- Van Valen, L., 1964. Relative abundance of species in some fossil mammal faunas. *Am. Nat.* 98, 109–116. <https://doi.org/10.1086/282307>.
- Vannier, J., 2012. Gut contents as direct indicators for trophic relationships in the Cambrian marine ecosystem. *PLoS One* 7, e25200. <https://doi.org/10.1371/journal.pone.0052200>.
- Velbel, M.A., Brandt, D.S., 1989. Differential preservation of brachiopod valves: taphonomic bias in *Platystrophia ponderosa*. *PALAIOS* 4, 193–195. <https://doi.org/10.2307/3514606>.
- Vendrasco, M.J., Porter, S.M., Kouchinsky, A.V., Li, G., Fernandez, C.Z., 2010. Shell microstructures in early mollusks. *The Festivus* 42, 43–53.
- Vermeij, G.J., 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* 3, 245–258. <https://doi.org/10.1017/S0094837300005352>.
- Vermeij, G.J., 1978. Biogeography and adaptation. Patterns of Marine Life. Harvard University Press, Cambridge and London.
- Vermeij, G.J., 1980. Drilling predation of bivalves in Guam: some paleoecological implications. *Malacologia* 19, 329–334.
- Vermeij, G.J., 1982a. Gastropod shell form, breakage, and repair in relation to predation by the crab *Calappa*. *Malacologia* 23, 1–12.
- Vermeij, G.J., 1982b. Unsuccessful predation and evolution. *Am. Nat.* 120, 701–720. <https://doi.org/10.1086/284025>.
- Vermeij, G.J., 1983. Traces and trends of predation, with special reference to bivalved animals. *Palaeontology* 26, 455–465.
- Vermeij, G.J., 1987. Evolution and Escalation: An Ecological History of Life. Princeton University Press.
- Vermeij, G.J., 1995. A Natural History of Shells. Princeton University Press, Princeton.
- Vermeij, G.J., 2017. Life in the arena: Infaunal gastropods and the late Phanerozoic expansion of marine ecosystems into sand. *Palaeontology* 60, 649–661. <https://doi.org/10.1111/pala.12310>.
- Vermeij, G.J., Dudley, E.C., 1982. Shell repair and drilling in some gastropods from the Ripley Formation (Upper Cretaceous) of the south-eastern U.S.A. *Cretac. Res.* 3, 397–403. [https://doi.org/10.1016/0195-6671\(82\)90041-6](https://doi.org/10.1016/0195-6671(82)90041-6).
- Vermeij, G.J., Herbert, G.S., 2004. Measuring relative abundance in fossil and living assemblages. *Paleobiology* 30, 1–4. [https://doi.org/10.1666/0094-8373\(2004\)030<0001:MRAIFA>2.0.CO;2](https://doi.org/10.1666/0094-8373(2004)030<0001:MRAIFA>2.0.CO;2).
- Vermeij, G.J., Williams, S.T., 2007. Predation and the geography of opercular thickness in turbinid gastropods. *J. Molluscan Stud.* 73, 67–73. <https://doi.org/10.1093/mollus/eyl032>.
- Vermeij, G.J., Schindel, D.E., Zipser, E., 1981. Predation through geological time: evidence from gastropod shell repair. *Science* 214, 1024–1026. <https://doi.org/10.1126/science.214.4524.1024>.
- Vermeij, G.J., Dudley, E.C., Zipser, E., 1989. Successful and unsuccessful drilling predation in Recent pelecypods. *The Veliger* 32, 266–273.
- Veron, J.E.N., 2008. Mass extinctions and ocean acidification: Biological constraints on geological dilemmas. *Coral Reefs* 27, 459–472. <https://doi.org/10.1007/s00338-008-0381-8>.
- Vignali, R., Galleni, L., 1986. Naticid predation on soft bottom bivalves: a study on a beach shell assemblage. *Oebalia* 13, 157–178.
- Villegas-Martín, J., Rojas-Consuegra, R., Klompmaker, A.A., 2016. Drill hole predation on tubes of serpulid polychaetes from the Upper Cretaceous of Cuba. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 455, 44–52. <https://doi.org/10.1016/j.palaeo.2016.05.009>.
- Villegas-Martín, J., Ceolin, D., Fauth, G., Klompmaker, A.A., 2019. A small yet occasional meal: Predatory drill holes in Paleocene ostracods from Argentina and methods to infer predation intensity. *Palaeontology*. <https://doi.org/10.1111/pala.12423>.
- Vinn, O., 2009. Attempted predation on Early Paleozoic cornulitids. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 273, 87–91. <https://doi.org/10.1016/j.palaeo.2008.12.004>.
- Vinn, O., 2012. Shell repair in *Anticalyptraea* (Tentaculita) in the late Silurian (Pridoli) of Baltica. *Carnets de Géologie* 31–37 2012/01.
- Viohl, G., 1990. Piscivorous fishes of the Solnhofen lithographic limestone. In: Boucot, A.J. (Ed.), *Evolutionary Paleobiology of Behaviour and Coevolution*. Elsevier, Amsterdam, pp. 287–304.
- Visaggi, C.C., Kelley, P.H., 2015. Equatorward increase in naticid gastropod drilling predation on infaunal bivalves from Brazil with paleontological implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 438, 285–299. <https://doi.org/10.1016/j.palaeo.2016.05.009>.

- palaeo.2015.07.045.
- Visaggi, C.C., Dietl, G.P., Kelley, P.H., 2013. Testing the influence of sediment depth on drilling behaviour of *Neverita duplicata* (Gastropoda: Naticidae), with a review of alternative modes of predation by naticids. *J. Molluscan Stud.* 79, 310–322. <https://doi.org/10.1093/mollus/eyt023>.
- Voight, J.R., 2000. A review of predators and predation at deep-sea hydrothermal vents. *Cah. Biol. Mar.* 41, 155–166.
- Voigt, E., 1975. Tunnelbaue rezenter und fossiler Phoronidea. *Paläontol. Z.* 49, 135–167. <https://doi.org/10.1007/BF02988072>.
- Voss, M., Antar, M.S.M., Zalmout, I.S., Gingerich, P.D., 2019. Stomach contents of the archaeocete *Basilosaurus isis*: apex predator in oceans of the late Eocene. *PLoS One* 14, e0209021. <https://doi.org/10.1371/journal.pone.0209021>.
- Vullo, R., Cavin, L., Clochard, V., 2009. An ammonite-fish association from the Kimmeridgian (Upper Jurassic) of La Rochelle, western France. *Lethaia* 42, 462–468. <https://doi.org/10.1111/j.1502-3931.2009.00153.x>.
- Wahl, W.R., 2005. A hyodont shark from the Redwater Shale Member, Sundance Formation (Jurassic), Natrona County, Wyoming. *Paludicola* 5, 15–19.
- Waldbusser, G.G., Steenson, R.A., Green, M.A., 2011. Oyster shell dissolution rates in estuarine waters: Effects of pH and shell legacy. *J. Shellfish Res.* 30, 659–669. <https://doi.org/10.2983/035.030.0308>.
- Walker, S.E., 2001. Paleoecology of gastropods preserved in turbiditic slope deposits from the Upper Pliocene of Ecuador. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 166, 141–163. [https://doi.org/10.1016/S0031-0182\(00\)00206-6](https://doi.org/10.1016/S0031-0182(00)00206-6).
- Walker, S.E., Behrens Yamada, S., 1993. Implications for the gastropod fossil record of mistaken crab predation on empty mollusc shells. *Palaeontology* 36, 735–741.
- Walker, S.E., Brett, C.E., 2002. Post-Paleozoic patterns in marine predation: was there a Mesozoic and Cenozoic marine predatory revolution? *Paleontol. Soc. Pap.* 8, 119–194. <https://doi.org/10.1017/S108933260000108X>.
- Walker, S.E., Voight, J.R., 1994. Paleoeologic and taphonomic potential of deepsea gastropods. *PALAIOS* 9, 48–59. <https://doi.org/10.2307/3515078>.
- Walker, S.E., Parsons-Hubbard, K., Powell, E., Brett, C.E., 2002. Predation on experimentally deployed molluscan shells from shelf to slope depths in a tropical carbonate environment. *PALAIOS* 17, 147–170. [https://doi.org/10.1669/0883-1351\(2002\)017<0147:POEDMS>2.0.CO;2](https://doi.org/10.1669/0883-1351(2002)017<0147:POEDMS>2.0.CO;2).
- Walker, S.E., Hancock, L.G., Bowser, S.S., 2017. Diversity, biogeography, body size and fossil record of parasitic and suspected parasitic Foraminifera: a review. *J. Foraminif. Res.* 47, 34–55. <https://doi.org/10.2113/gsjfr.47.1.34>.
- Wani, R., 2004. Experimental fragmentation patterns of modern *Nautilus* shells and the implications for fossil cephalopod taphonomy. *Lethaia* 37, 113–123. <https://doi.org/10.1080/00241160410006420>.
- Ward, P., 1981. Shell sculpture as a defensive adaptation in ammonoids. *Paleobiology* 7, 96–100. <https://doi.org/10.1017/S009483730000381X>.
- Ward, P.D., Martin, A.W., 1980. Depth distribution of *Nautilus pompilius* in Fiji and *Nautilus macromphalus* in New Caledonia. *The Veliger* 22, 259–264.
- Ware, D.M., 1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density, and prey size. *J. Fish. Res. Board Can.* 29, 1193–1201. <https://doi.org/10.1139/f72-175>.
- Warén, A., 1981. Eulimid gastropods parasitic on echinoderms in the New Zealand region. *N. Z. J. Zool.* 8, 313–324. <https://doi.org/10.1080/03014223.1981.10430611>.
- Warén, A., Crossland, M.R., 1991. Revision of *Hypermastus* Pilsbry, 1899 and *Turveria* Berry, 1956 (Gastropoda: Prosobranchia: Eulimidae), two genera parasitic on sand dollars. *Rec. Aust. Mus.* 43, 85–112.
- Warén, A., Norris, D.R., Templado, J., 1994. Descriptions of four new eulimid gastropods parasitic on irregular sea urchins. *The Veliger* 37, 141–154.
- Webb, G.E., Yancey, T.E., 2010. Skeletal repair of extreme damage in rugose corals, Pella Formation (Mississippian, Iowa, USA). *Palaeoworld* 19, 325–332. <https://doi.org/10.1016/j.palwor.2010.08.005>.
- Weissburg, M.J., Zimmer-Faust, R.K., 1993. Life and death in moving fluids: Hydrodynamic effects on chemosensory-mediated predation. *Ecology* 74, 1428–1443. <https://doi.org/10.2307/1940072>.
- Whittle, R.J., Quaglio, F., Griffiths, H.J., Linse, K., Crame, J.A., 2014. The Early Miocene Cape Melville Formation fossil assemblage and the evolution of modern Antarctic marine communities. *Naturwissenschaften* 101, 47–59. <https://doi.org/10.1007/s00114-013-1128-0>.
- Williams, M.E., 1990. Feeding behavior in Cleveland Shale fishes. In: Boucot, A.J. (Ed.), *Evolutionary Paleobiology of Behaviour and Coevolution*. Elsevier, Amsterdam, pp. 273–287.
- Wilson, W.H., 1991. Competition and predation in marine soft-sediment communities. *Annu. Rev. Ecol. Syst.* 21, 221–241. <https://doi.org/10.1146/annurev.es.21.110190.001253>.
- Wilson, M.A., 1998. Succession in a Jurassic marine cavity community and the evolution of cryptic marine faunas. *Geology* 26, 379–381. [https://doi.org/10.1130/0091-7613\(1998\)026<0379:SIJMC>2.3.CO;2](https://doi.org/10.1130/0091-7613(1998)026<0379:SIJMC>2.3.CO;2).
- Wilson, M.A., Palmer, T.J., 2001. Domiciles, not predatory borings: a simpler explanation of the holes in Ordovician shells analyzed by Kaplan and Baumiller, 2000. *PALAIOS* 16, 524–525. [https://doi.org/10.1669/0883-1351\(2001\)016<0524:DNPBAS>2.0.CO;2](https://doi.org/10.1669/0883-1351(2001)016<0524:DNPBAS>2.0.CO;2).
- Wilson, M.A., Taylor, P.D., 2006. Predatory drill holes and partial mortality in Devonian colonial metazoans. *Geology* 34, 565–568. <https://doi.org/10.1130/G22468.1>.
- Wilson, M.A., Borszcz, T., Zatoń, M., 2015. Bitten spines reveal unique evidence for fish predation on Middle Jurassic echinoids. *Lethaia* 48, 4–9. <https://doi.org/10.1111/let.12110>.
- Wiltse, W.I., 1980. Predation by juvenile *Polinices duplicatus* (Say) on *Gemma gemma* (Totten). *J. Exp. Mar. Biol. Ecol.* 42, 187–199. [https://doi.org/10.1016/0022-0981\(80\)90175-6](https://doi.org/10.1016/0022-0981(80)90175-6).
- Wissihak, M., Neumann, C., Jakobsen, J., Freiwald, A., 2009. The 'living-fossil community' of the cyrtocrinid *Cyathidium foresti* and the deep-sea oyster *Neopycnodonte zibrowii* (Azores Archipelago). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 271, 77–83. <https://doi.org/10.1016/j.palaeo.2008.09.015>.
- Wissihak, M., Titschack, J., Kahl, W.-A., Girod, P., 2017. Classical and new bioerosion trace fossils in Cretaceous belemnite guards characterised via micro-CT. *Foss. Rec.* 20, 173–199. <https://doi.org/10.5194/fr-20-173-2017>.
- Wodinsky, J., 1969. Penetration of the shell and feeding on gastropods by *Octopus*. *Am. Zool.* 9, 997–1010. <https://doi.org/10.1093/icb/9.3.997>.
- Woelke, C.E., 1957. The flatworm *Pseudostylochus ostreophagus* Hyman, a predator of oysters. *Proc. Natl. Shellfish. Assoc.* 47, 62–67.
- Wood, L., 1968. Physiological and ecological aspects of prey selection by the marine gastropod *Urosalpinx cinera* (Prosobranchia: Muricidae). *Malacologia* 6, 167–320.
- Wood, R., 1999. *Reef Evolution*. Oxford University Press, Oxford.
- Wood, R., 2003. Predation in ancient reef-builders. In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), *Predator-Prey Interactions in the Fossil Record*, Topics in Geobiology. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp. 33–53. https://doi.org/10.1007/978-1-4615-0161-9_3.
- Wood, J.E., Wilmshurst, J.M., Wagstaff, S.J., Worthy, T.H., Rawlence, N.J., Cooper, A., 2012. High-resolution coproecology: using coprolites to reconstruct the habits and habitats of New Zealand's extinct upland moa (*Megalapteryx didinus*). *PLoS One* 7, e40025. <https://doi.org/10.1371/journal.pone.0040025>.
- Worm, B., Sandow, M., Oschlies, A., Lotze, H.K., Myers, R.A., 2005. Global patterns of predator diversity in the open oceans. *Science* 309, 1365–1369. <https://doi.org/10.1126/science.1113399>.
- Wretman, L., Kearn, B.P., 2014. Bite marks on an ichthyodectiform fish from Australia: possible evidence of trophic interaction in an Early Cretaceous marine ecosystem. *Alcheringa* 38, 170–176. <https://doi.org/10.1080/03115518.2014.848692>.
- Wright, C.W., Wright, E.V., 1940. Notes on Cretaceous Asteroidea. *Q. J. Geol. Soc.* 96, 231–248. pls 13–17. <https://doi.org/10.1144/GSL.JGS.1940.096.01-04.08>.
- Wright, P., Cherns, L., Hodges, P., 2003. Missing molluscs: Field testing taphonomic loss in the Mesozoic through early large-scale aragonite dissolution. *Geology* 31, 211–214. [https://doi.org/10.1130/0091-7613\(2003\)031<0211:MMFTTL>2.0.CO;2](https://doi.org/10.1130/0091-7613(2003)031<0211:MMFTTL>2.0.CO;2).
- Wright, J.M., Parker, L.M., O'Connor, W.A., Williams, M., Kube, P., Ross, P.M., 2014. Populations of Pacific oysters *Crassostrea gigas* respond variably to elevated CO₂ and predation by *Morula marginalba*. *Biol. Bull.* 226, 269–281. <https://doi.org/10.1086/BBLv226n3p269>.
- Wu, F., Wang, T., Cui, S., Xie, Z., Dupont, S., Zeng, J., Gu, H., Kong, H., Hu, M., Lu, W., Wang, Y., 2017. Effects of seawater pH and temperature on foraging behavior of the Japanese stone crab *Charybdis japonica*. *Mar. Pollut. Bull.* 120, 99–108. <https://doi.org/10.1016/j.marpolbul.2017.04.053>.
- Yang, J., Smith, M.R., Lan, T., Hou, J., Zhang, X., 2014. Articulated *Wiwaxia* from the Cambrian Stage 3 Xiaoshiba Lagerstätte. *Sci. Rep.* 4, 4643. <https://doi.org/10.1038/srep04643>.
- Yochelson, E.L., 1979. Gastropod opercula as objects for paleobiogeographic study. In: Gray, J., Boucot, A.J. (Eds.), *Historical Biogeography, Plate Tectonics, and the Changing Environment*. Proceedings of the Annual Biology Colloquium and Selected Papers, pp. 37–43.
- Yochelson, E.L., Dockery, D., Wolf, H., 1983. Predation of sub-Holocene scaphopod mollusks from southern Louisiana. *Geol. Surv. Prof. Pap.* 1282, 1–13 4 pls.
- Yonge, C.M., 1964. Rock borers. *Sea Front* 10, 106–116.
- Young, D.K., 1969. *Okadaia elegans*, a tube-boring nudibranch mollusc from the central and west Pacific. *Am. Zool.* 9, 903–907.
- Zachos, J.C., Röhl, U., Schellenberg, S.A., Sluijs, A., Hodell, D.A., Kelly, D.C., Thomas, E., Nicolo, M., Raffi, I., Lourens, L.J., 2005. Rapid acidification of the ocean during the Paleocene-Eocene Thermal Maximum. *Science* 308, 1611–1615. <https://doi.org/10.1126/science.1109004>.
- Zakharenko, G.V., 2008. Possible evidence of predation in placoderms (Pisces) of the Evlanovo basin of central Russia. *Paleontol. J.* 42, 522–525. <https://doi.org/10.1134/S0013030108050079>.
- Zangerl, R., Richardson, E.S., 1963. *The Paleoeological History of Two Pennsylvanian Black Shales*, Fieldiana: Geology Memoirs 8. Chicago Natural History Museum, Chicago.
- Zatoń, M., Rakociński, M., 2014. Coprolite evidence for carnivorous predation in a Late Devonian pelagic environment of southern Laurussia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 394, 1–11. <https://doi.org/10.1016/j.palaeo.2013.11.019>.
- Zatoń, M., Salamon, M.A., 2008. Durophagous predation on Middle Jurassic molluscs, as evidenced from shell fragmentation. *Palaeontology* 51, 63–70. <https://doi.org/10.1111/j.1475-4983.2007.00736.x>.
- Zatoń, M., Villier, L., Salamon, M.A., 2007. Signs of predation in the Middle Jurassic of south-central Poland: evidence from echinoderm taphonomy. *Lethaia* 40, 139–151. <https://doi.org/10.1111/j.1502-3931.2007.00017.x>.
- Zatoń, M., Salamon, M.A., Boczarowski, A., Sitek, S., 2008. Taphonomy of dense ophiuroid accumulations from the Middle Triassic of Poland. *Lethaia* 41, 47–58. <https://doi.org/10.1111/j.1502-3931.2007.00041.x>.
- Zatoń, M., Broda, K., Qvarnström, M., Niedźwiedzki, G., Ahlberg, P.E., 2017. The first direct evidence of a Late Devonian coelacanth fish feeding on conodont animals. *Sci. Nat.* 104, 26. <https://doi.org/10.1007/s00114-017-1455-7>.

- Zhu, M.-Y., Vannier, J., Van Iten, H., Zhao, Y.-L., 2004. Direct evidence for predation on trilobites in the Cambrian. *Proc. R. Soc. B Biol. Sci. Suppl.* 271, S277–S280.
- Ziegelmeier, E., 1954. Beobachtungen über den Nahrungserwerb bei der Naticide *Lunatia nitida* Donovan (Gastropoda Prosobranchia). *Helgoländer Wiss. Meeresunters.* 5, 1–33.
- Zinsmeister, W.J., 1980. Observations on the predation of the clypeastroid echinoid, *Monophoraster darwini*, from the Upper Miocene Entrerrios Formation, Patagonia, Argentina. *J. Paleontol.* 54, 910–912.
- Zintzen, V., Rogers, K.M., Roberts, C.D., Stewart, A.L., Anderson, M.J., 2013. Hagfish feeding habits along a depth gradient inferred from stable isotopes. *Mar. Ecol. Prog. Ser.* 485, 223–234. <https://doi.org/10.3354/meps10341>.
- Złotnik, M., 2001. Size-related changes in predatory behaviour of naticid gastropods from the Middle Miocene Korytnica Clays, Poland. *Acta Palaeontol. Pol.* 46, 87–97.
- Złotnik, M., Ceranka, T., 2005. Patterns of drilling predation of cassid gastropods preying on echinoids from the Middle Miocene of Poland. *Acta Palaeontol. Pol.* 50, 409–428.
- Zong, R.-W., Fan, R.-Y., Gong, Y.-M., 2016. Seven 365-million-year-old trilobites moulting within a nautiloid conch. *Sci. Rep.* 6, 34914. <https://doi.org/10.1038/srep34914>.
- Zuschin, M., Ebner, C., 2015. Actupaleontological characterization and molluscan biodiversity of a protected tidal flat and shallow subtidal at the northern Red Sea. *Facies* 61, 5. <https://doi.org/10.1007/s10347-015-0428-6>.
- Zuschin, M., Stanton, R.J., 2001. Experimental measurement of shell strength and its taphonomic interpretation. *PALAIOS* 16, 161–170. [https://doi.org/10.1669/0883-1351\(2001\)016<0161:EMOSSA>2.0.CO;2](https://doi.org/10.1669/0883-1351(2001)016<0161:EMOSSA>2.0.CO;2).
- Zuschin, M., Stachowitsch, M., Stanton, R.J., 2003. Patterns and processes of shell fragmentation in modern and ancient marine environments. *Earth-Sci. Rev.* 63, 33–82. [https://doi.org/10.1016/S0012-8252\(03\)00014-X](https://doi.org/10.1016/S0012-8252(03)00014-X).